Individual Responses of Adult Little Owls (*Athene noctua*) to Environmental Conditions

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Summary

Life-history theory predicts that individuals need to adjust their behaviour to specific environmental conditions in order to maximise their fitness. Thus, to understand how the environment affects demography and population dynamics, it is crucial to study the behavioural responses of individuals to different aspects of the environment as well as the consequences of these responses for reproduction and survival. Two aspects of the environment affect animals across all life-history stages. First, the availability of food resources determines the amount of energy available for different life-history functions. If resources are limited during the breeding season, parents need to decide how to allocate limited energy among reproduction and self-maintenance. As a result, individuals may adjust breeding site selection, range use, home-range size, or parental effort to the availability of food. Second, predators influence population dynamics and the spatial distribution of animals directly by lethal predation and indirectly by eliciting anti-predator behaviours.

In this thesis, I used the little owl (*Athene noctua*) as a study system to investigate three issues faced by adult animals: the allocation of energy between reproduction and self-maintenance as a function of the habitat conditions (Chapters 1-3), the decision between philopatry and breeding dispersal (Chapter 4), and the behavioural response to predation risk (Chapter 5). Using very high frequency (VHF) radio-telemetry, I tracked individuals throughout the year, allowing me to calculate season-specific home-range sizes and survival rates with a high temporal resolution. A nestling food supplementation experiment enabled me to investigate parental responses to the nutritional state of the nestlings and to evaluate food limitation of reproduction in habitats of different quality.

In **Chapter 1**, I showed that, irrespective of the parental home-range size, clutch size was positively correlated with the proportion of food-rich habitat close to the nest,

suggesting that the distance between high quality food resources and suitable nest sites plays an important role for the productivity of little owls. Paternal home-range size was positively correlated with the survival of the father and the nestlings. In homogenous landscapes, parents seem to expand their home-range to include additional food-rich habitat, thereby gaining a net benefit in terms of reproductive success and parental survival. In **Chapter 2**, I showed that nestlings in poor habitats only received two thirds of the biomass delivered to nests in high-quality habitats, resulting in lower survival of nestlings in poor habitats. Food supplementation increased the survival of adult males and females, not only during the breeding season but also during the following periods of the year, suggesting that little owl parents are limited by the availability of food resources (**Chapter 3**). Thus, the first three chapters of this thesis provide insights into the mechanisms regulating the trade-off between current reproduction and self-maintenance under varying habitat conditions. I conclude from the results that habitats of low quality affect individual life histories and local demographic rates both in the short term (reduced current reproductive output), and in the long term (reduced survival prospects and future reproductive success of adults).

In **Chapter 4**, I investigated the patterns, proximate causes and consequences of breeding dispersal. Little owls showed an overall dispersal rate of 20% from one year to the next. Reproductive failure strongly increased the propensity of individuals to disperse. In addition, individuals that had already shown breeding dispersal were more likely than others to change their territory again. On average the reproductive success of dispersers was similar to philopatric individuals, but dispersers reared 0.6 fledglings more after dispersal compared to the preceding year. Our data confirm the strong site fidelity of adult little owls, with 98% of the little owls staying within 2 km of their previous nest site. However, depending on habitat-linked brood loss, the rates of breeding dispersal may be

considerable. Therefore, I suggest that breeding dispersal strongly contributes to the small scale dynamics and turn-over within little owl populations.

Finally, in **Chapter 5**, I used the playback of little owl and tawny owl (*Strix aluco*) calls to model the site occupancy of the two species across the whole study area and to test whether the distribution of tawny owls affects the distribution of little owls. Site occupancy of little owls strongly decreased within 150 m from the forest in the presence, but not in the absence of tawny owls. In addition, little owls strongly avoided areas closer than 150 m to forest edges during their night-time range use. These results suggest that little owls perceive the predation risk caused by tawny owls and adapt their spatial behaviour accordingly.

I draw two main conclusions from this PhD thesis. First, habitat-specific food supply during the breeding season is of crucial importance for both juveniles and adults. On one hand, it strongly affects productivity by regulating the clutch size as well as the survival of juveniles. On the other hand, it is an important determinant of the survival prospects of adults, thereby affecting lifetime reproductive success. On the individual level, nest site selection determines the access to resources. Thus, settlement decisions and habitat selection represent key ecological mechanisms affecting individual fitness. Second, both habitat characteristics and the presence of predators strongly influence the spatial distribution and dynamics of little owls. Site-occupancy patterns suggest that little owls settle in areas, which minimize predation and secure optimal food resources. Since breeding dispersal mainly occurred in response to reproductive failure, habitat characteristics linked to reproductive failure further affect local population structure and dynamics. In conclusion, the results provide insights into the ecological mechanisms that shape the spatial distribution and the turn-over of individuals within a population.

Zusammenfassung

Die Life-History-Theorie sagt voraus, dass Individuen ihr Verhalten an spezifische Umweltbedingungen anpassen müssen, um ihre Fitness zu maximieren. Um zu verstehen wie die Umwelt die Demografie und die Populationsdynamik beeinflusst, ist es essenziell zu untersuchen, wie Individuen ihr Verhalten an verschiedene Umweltaspekte anpassen und wie sich diese Verhaltensweisen auf die Fortpflanzung und das Überleben auswirken. Zwei Umweltaspekte beeinflussen Tiere während all ihrer Lebensabschnitte. Erstens bestimmt die Verfügbarkeit von Nahrungsressourcen, wie viel Energie für die verschiedenen Lebensprozesse zur Verfügung steht. Im Falle begrenzter Nahrungsressourcen während der Brutzeit müssen die Eltern entscheiden, wie sie die limitierte Energie zwischen Reproduktion und Selbsterhaltung aufteilen. Folglich kann es sein, dass Brutplatzwahl, Raumnutzung, Reviergrösse elterliche Anstrengungen an das Vorhandensein von Futter angepasst werden. Zweitens beeinflussen Fressfeinde die Populationsdynamik und die räumliche Verteilung von Tieren direkt durch Prädation sowie indirekt indem sie Feindvermeidungsverhalten auslösen.

In dieser Arbeit habe ich den Steinkauz (*Athene noctua*) als Modellorganismus genutzt, um drei Probleme, die sich Alttieren stellen, zu untersuchen: Die Energieverteilung zwischen Selbsterhaltung und Fortpflanzung in Abhängigkeit der Habitatbedingungen (Kapitel 1-3), die Entscheidung zwischen Brutortstreue und Brutplatzwechsel (Kapitel 4) und die Verhaltensantwort auf Prädationsrisiko (Kapitel 5).

Mit Hilfe von VHF (very high frequency) Radio-Telemetrie habe ich die Individuen während des ganzen Jahres verfolgt, was es mir ermöglichte, jahreszeitspezifische Reviergrössen und Überlebensraten mit einer hohen zeitlichen Auflösung zu berechnen. Ein Nestlings-Zufütterungs-Experiment erlaubte es mir zu untersuchen, wie die Eltern ihr

Verhalten an den Ernährungszustand der Nestlinge anpassen, und zu ermitteln inwiefern die Fortpflanzung durch Futterknappheit in Habitaten verschiedener Qualität limitiert ist.

Im **ersten Kapitel** konnte ich zeigen, dass die Gelegegrösse positiv mit dem Anteil von futterreichem Habitat in Nestnähe korreliert war und zwar unabhängig von der elterlichen Reviergrösse. Dieses Resultat weist darauf hin, dass die Distanz zwischen Nahrungsressourcen hoher Qualität und geeigneten Brutplätzen eine wichtige Rolle für die Produktivität von Steinkäuzen spielt. Die elterliche Reviergrösse war positiv mit dem Überleben des Vaters und der Nestlinge korreliert. In homogenen Landschaften scheinen Altvögel ihr Revier zu vergrössern, um zusätzliches futterreiches Habitat einzuschliessen, was sich vorteilhaft auf den Reproduktionserfolg und das elterliche Überleben auswirkt. Im **zweiten Kapitel** konnte ich zeigen, dass Nestlinge in schlechten Habitaten lediglich zwei Drittel der Biomasse erhielten, welche in Habitaten hoher Qualität zum Nest gebracht wurde. Dies führte zu einer höheren Nestlingssterblichkeit in schlechten Habitaten. Die Zufütterung erhöhte das Überleben von männlichen und weiblichen Altvögeln, nicht nur während der Brutzeit, sondern auch in den darauffolgenden Abschnitten des Jahres. Dies deutet darauf hin, dass Steinkauz-Eltern durch die Verfügbarkeit von Nahrungsressourcen limitiert werden (**Kapitel 3**). Die ersten drei Kapitel dieser Arbeit gewähren Einblicke in die Mechanismen, welche den Trade-Off zwischen aktueller Fortpflanzung und Selbsterhaltung in verschiedenen Umwelbedingungen regulieren. Aus den Resultaten folgere ich, dass Habitate geringer Qualität die individuellen Lebensprozesse und lokalen demografischen Raten sowohl kurzzeitig (reduzierter aktueller Bruterfolg) als auch langfristig (reduzierte Überlebensaussichten und zukünftiger Bruterfolg) beeinflussen.

Im **vierten Kapitel** untersuchte ich die Muster, direkten Ursachen und Konsequenzen von Brutplatzwechseln. Insgesamt zeigten Steinkäuze eine Wechselrate von 20% von einem Jahr zum nächsten. Misserfolge bei der Reproduktion erhöhten die Tendenz zu einem Brutplatzwechsel stark. Ausserdem wechselten Individuen, die zuvor

bereits einen Brutplatzwechsel vorgenommen hatten, häufiger erneut den Brutplatz als andere Individuen. Der durchschnittliche Bruterfolg von wechselnden und ortstreuen Tieren war ähnlich. Jedoch waren die Tiere, welche einen Brutplatzwechsel vollzogen hatten, nach dem Wechsel erfolgreicher bei der Jungenaufzucht als im Vorjahr (im Durchschnitt 0.6 zusätzliche Flügglinge). Unsere Daten bestätigen die grosse Ortstreue adulter Steinkäuze: 98% der Brutvögel blieben innerhalb von 2 km des vorhergehenden Brutplatzes. Trotzdem kann die Wechselrate in Habitaten mit erhöhtem Brutverlust beträchtlich sein. Deshalb schlage ich vor, dass Brutplatzwechsel stark zur kleinräumigen Dynamik und zum Turn-Over in Steinkauzpopulationen beitragen können.

Im **fünften Kapitel** habe ich Playbacks von Steinkauz- und Waldkauzrufen (*Strix aluco*) benutzt, um die Revierbelegung der beiden Arten im gesamten Studiengebiet zu modellieren und um zu testen, ob die Verteilung der Waldkäuze die Verteilung der Steinkäuze beeinflusst. Das Vorkommen der Steinkäuze war in einem Abstand von 150 m des Walds stark verringert wenn Waldkäuze vorhanden waren, aber nicht in deren Abwesenheit. Ausserdem wurden Zonen, die sich näher als 150 m am Waldrand befinden, von Steinkäuzen während ihrer nächtlichen Ausflüge stark gemieden. Diese Resultate suggerieren, dass die Steinkäuze das vom Waldkauz ausgehende Prädations-Risiko wahrnehmen und ihr räumliches Verhalten dementsprechend anpassen.

Ich ziehe zwei wesentliche Schlussfolgerungen aus dieser Doktorarbeit. Erstens, das Habitat-abhängige Futterangebot während der Brutzeit ist essentiell für das Überleben der juvenilen und adulten Steinkäuze. Einerseits beeinflusst es die Produktivität stark, indem es sowohl die Gelegegrösse als auch das Überleben der Nestlinge reguliert. Andererseits ist es ein starker Bestimmungsfaktor der Überlebensaussichten der Adultvögel, und beeinflusst somit den totalen Bruterfolg während der gesamten Lebensdauer. Auf der Ebene des Individuums bestimmt die Wahl des Brutplatzes den Zugang zu Ressourcen. Daher sind Brutplatzwahl und Habitat-Nutzung ökologische Schlüsselmechanismen,

welche die individuelle Fitness beeinflussen. Zweitens, sowohl Habitatsmerkmale als auch die Anwesenheit von Fressfeinden beeinflussen die räumliche Verteilung und Dynamik des Steinkauzes stark. Die Verteilungs-Muster legen nahe, dass sich Steinkäuze in Gebieten niederlassen, wo der Prädationsdruck minimal ist und optimale Futterquellen gesichert sind. Da Brutplatzwechsel hauptsächlich auf Misserfolge bei der Reproduktion zurückzuführen waren, beeinflussen Habitat-Merkmale, welche zu Brutverlust führen können, die lokale Populationsstruktur und Dynamik zusätzlich. Zusammenfassend gewähren die Resultate dieser Arbeit Einblicke in die ökologischen Mechanismen, welche die räumliche Verteilung und den Turn-Over der Individuen in einer Population prägen.

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General introduction

Life-history theory predicts that selection maximises individual lifetime reproductive success via flexible responses to environmental conditions (Stearns 1992). Behavioural plasticity allows animals to cope with changing conditions (Nussey *et al.* 2007). Particularly in fast changing landscapes altered by humans, such as farmland, plastic behaviour may be important for population persistence (Tuomainen & Candolin 2011). Studying the behavioural adjustments of individuals to environmental conditions throughout the annual cycle as well as the consequences of these behaviours on reproductive output and survival is crucial to understanding how the environment affects demographic rates and population dynamics.

Depending on the life-history stage, various aspects of the environment may induce differential behavioural responses. The availability of food within the landscape affects animals across all life-history stages by determining the amount of energy available for different life-history functions (van Noordwijk & de Jong 1986). Thus, both the reproductive output and the survival of adults are positively correlated with the availability of food. Under constraints from limited resources, a fundamental trade-off in allocation of energy among reproduction and self-maintenance occurs (Stearns 1989; Clutton-Brock 1991). In addition, the distribution of food-rich habitat patches and the accessibility of food within these patches shape the range use and spatial behaviour of individuals (Fuller 2012).

During foraging, individuals also need to adjust their behaviour to habitat-specific predation risk. Predators influence population dynamics and the spatial distribution of animals directly by lethal predation and indirectly via risk effects (Lima & Dill 1990; Creel & Christianson 2008). Individuals are expected to adjust their behaviour to spatial variation in predation risk (Brown *et al.* 1999; Laundré *et al.* 2001). Thus, the effect of predators on

prey population dynamics may be regarded as a feed-back cycle between predator impact and anti-predator adaptations of prey.

For reproduction, many species are confined to specific suitable sites (e.g. dens, burrows, cavities or nest sites). In territorial species, parents can ensure the access to sufficient resources for both their offspring and themselves by selecting a site surrounded by favourable habitat for reproduction (Korpimäki 1988). As a result, there may be strong competition for high quality breeding sites (e.g. Gustafsson 1988). Thus, territory holders need to defend their territory against intruders. After each reproductive cycle, individuals need to decide whether to stay at the same site for a subsequent reproductive attempt, or to move to a different territory. Thus, in addition to food availability and predation risk, competition for the breeding site, personal experience, and previous reproductive success are also expected to affect the decision between philopatry and breeding dispersal (Forero *et al.* 1999; Calabuig *et al.* 2008). How individual dispersal decisions affect population dynamics is expected to depend on the ratio between costs and benefits of dispersal.

In this thesis, I use the little owl (*Athene noctua*) as a model system to investigate how food availability and predation risk shape the behaviour of adult individuals, the resulting spatial patterns, and the consequences of these behavioural adjustments for reproductive output and adult survival.

Behavioural responses to variation in food supply

Females of many bird species adjust their clutch size to the availability of food within their territory (Drent & Daan 1980; Korpimäki & Hakkarainen 1991). In addition, both females and males may adjust the effort for foraging and provisioning of the young to specific environmental conditions (Schifferli *et al.* 2014). Depending on landscape heterogeneity and competition, the use of a larger home-range may provide access to additional resources. Thus, the amount of energy delivered to the nest, which is a function of

parental effort and the quality of the habitat, is expected to determine the number, survival, and condition of the young.

While the flow of energy to the brood affects the survival and condition of the nestlings, high provisioning rates are expected to be costly for the parents. Particularly if resources are limited, parents need to decide how to allocate energy among reproduction and self-maintenance. Fitness costs of reproduction may include reduced adult survival (Nur 1984; Daan *et al.* 1996), delayed breeding in the subsequent year (Røskaft 1985; Brommer *et al.* 2004), or reduced future reproductive output (Nur 1988; Hanssen *et al.* 2005). Although many studies have addressed the costs of reproduction, the direct relationship between habitat-dependent parental effort and future fitness consequences remains poorly understood.

Predation pressure as a driver of spatial patterns

In addition to food, predation is another key ecological factor shaping individual behaviour, reproductive output, and adult survival. There is strong selection for efficient anti-predator behaviours because individuals that do not show such behaviours incur greater mortality. By killing prey individuals, predators directly affect prey demography. In addition, non-lethal effects include increased vigilance during foraging, which reduces foraging efficiency, or changes in the spatial behavior of prey such as avoidance of areas of high predation risk (Lima & Dill 1990; Cresswell *et al.* 2010). These risk-minimising responses are expected to be costly for prey individuals (Creel & Christianson 2008).

Habitat segregation between prey and predator may mitigate the negative effects of predation risk by reducing the encounter rates of the two species. However, it remains unclear if reduced occupancy near habitat edges is due to direct predation, due to edge avoidance in response to perceived predation risk, or both (Suhonen *et al.* 1994; Lima

2009; Fonderflick *et al.* 2013). Behavioural studies are needed to differentiate between the two mechanisms (Lima & Valone 1991).

This thesis

General approach

To understand how environmental conditions affect reproductive success, spatial dynamics, and the survival of parents, it is necessary to investigate how individuals adjust their behaviour to these environmental conditions. In my PhD, I focus on three key issues faced by adult animals in the course of their life: (1) the trade-off between reproduction and self-maintenance, (2) the decision between philopatry and breeding dispersal, and (3) the behavioural response to predation risk. Very high frequency (VHF) radio-telemetry was used to track individuals throughout the year, allowing me to calculate season-specific home-range sizes. These home-range sizes were then used to investigate how little owls adjust their home-range to different habitat characteristics, and if the reproductive output is linked to parental home-range size. During the nestling stage, feeding rates and prey composition in habitats of different quality were quantified. In addition, I used a nestling food supplementation experiment to manipulate the food supply compared to control nests, allowing me to investigate parental responses to the nutritional state of the nestlings and food limitation of reproduction in habitats of different quality. Telemetry also allowed me to calculate survival rates of adults with a high temporal resolution and to test the effect of experimentally increased nestling food supply on parental survival. A combination of our telemetry data with ringing data from five long-term studies in Germany and one study in the Netherlands allowed me to investigate the patterns, proximate causes and consequences of breeding dispersal. Following individuals of both prey and predator species is very time consuming and cost-intensive. Site-occupancy models based on survey data provide a cost-efficient method to gather data across a large area and multiple

species. Consequently, I used the playback of little owl and tawny owl (*Strix aluco*) calls to estimate the site occupancy of the two species across our whole study area in two consecutive years.

Study species and study area

The little owl is a nocturnal owl living in open areas (Van Nieuwenhuyse *et al.* 2008). In Central Europe, it mostly occupies farmland habitats. Since it is highly territorial and stays within the same area throughout the year, it is very well suited to study how individuals adjust their behaviour to environmental conditions throughout the year. Previous studies have shown that little owls experience food limitation during the breeding season (Thorup *et al.* 2010; Perrig 2015), suggesting a strong trade-off between current reproduction and survival or future reproduction.

Since 1988, the little owl sub-population within our study area (district of Ludwigsburg, Southern Germany: 48°53′43″N, 9°11′45″E) has increased from eight to currently 220 known breeding pairs thanks to the placement of artificial nest boxes (H. Keil, unpublished data). Since the density is low compared to other areas (~ 0.55 breeding pairs per km^2: H. Keil, unpublished data, compared to a mean density ± 1 SD of 1.84 ± 5.25 breeding pairs per km^2 across 69 western European studies: Génot & Van Nieuwenhuyse 2002), density dependent effects are expected to be low. In addition, there is a surplus of nest boxes, reducing the limitation of breeding sites.

Outline of the thesis

This thesis consists of five papers. **Chapters one to three** are concerned with the reproductive ecology of the little owl from the perspective of the adults, whereas **chapter four** investigates breeding dispersal and **chapter five** examines predator avoidance behaviour.

In **chapter one**, I analyse how different aspects of heterogeneity of farmland affect the home-range size and reproductive success of little owls. The results give insights into the importance of landscape supplementation and landscape complementation (Dunning *et al.* 1992) for population productivity.

Chapter two uses a nestling food supplementation experiment to test how the food supply in habitats of different quality affects the feeding rates of adult little owls and the biomass delivered to the nest. A novel approach to estimate the detectability of different prey types on camera trap pictures allows accounting for imperfect detection of prey. It provides experimental evidence for the mechanisms, which link habitat quality with parental provisioning behaviour, thereby resulting in differential reproductive output.

In addition, the food supplementation experiment allowed me to investigate how constraints in natural food availability during the breeding season affect parental survival. Accordingly, in **chapter three** I test the hypothesis that reproduction is costly for the adults (in terms of survival prospects) and that additional food provided to the nestlings during the breeding season can reduce these costs.

In **chapter four** I investigate the importance of breeding dispersal for the spatial dynamics within little owl populations. Combining telemetry data and ring recoveries from six different long-term ringing projects, I use a Bayesian multi-state model to analyse the patterns and potential proximate causes of breeding dispersal. In addition, I compare the quality of the habitat before and after breeding dispersal, as well as the reproductive output between the two years to assess the potential benefits of breeding dispersal.

Chapter five investigates large scale site occupancy and spatial dynamics of little owls and their intraguild predator, the tawny owl (*Strix aluco*). Using an asymmetric, dynamic two-species occupancy model based on the site occupancy data, I analyse the impact of the distribution of tawny owls on the spatial distribution of little owls. Furthermore, I use telemetry data to test whether little owls avoid the forest edge.

References

Brommer, J.E., Karell, P. & Pietiäinen, H. (2004) Supplementary fed Ural owls increase their reproductive output with a one year time lag. *Oecologia*, **139,** 354-358.

Brown, J.S., Laundré, J.W. & Gurung, M. (1999) The ecology of fear: Optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy*, **80,** 385-399.

Calabuig, G., Ortego, J., Cordero, P.J. & Aparicio, J.M. (2008) Causes, consequences and mechanisms of breeding dispersal in the colonial lesser kestrel, *Falco naumanni*. *Animal Behaviour*, **76,** 1989-1996.

Clutton-Brock, T.H. (1991) *The evolution of parental care*. Princeton University Press, Princeton, USA.

Creel, S. & Christianson, D. (2008) Relationships between direct predation and risk effects. *Trends in Ecology & Evolution*, **23,** 194-201.

Cresswell, W., Lind, J. & Quinn, J.L. (2010) Predator-hunting success and prey vulnerability: Quantifying the spatial scale over which lethal and non-lethal effects of predation occur. *Journal of Animal Ecology*, **79,** 556-562.

Daan, S., Deerenberg, C. & Dijkstra, C. (1996) Increased daily work precipitates natural death in the kestrel. *Journal of Animal Ecology*, **65,** 539-544.

Drent, R.H. & Daan, S. (1980) The prudent parent: Energetic adjustments in avian breeding. *Ardea*, **68,** 225-252.

Dunning, J.B., Danielson, B.J. & Pulliam, H.R. (1992) Ecological processes that affect populations in complex landscapes. *Oikos*, **65,** 169-175.

Fonderflick, J., Besnard, A. & Martin, J.L. (2013) Species traits and the response of open-habitat species to forest edge in landscape mosaics. *Oikos*, **122,** 42-51.

Forero, M.G., Donázar, J.A., Blas, J. & Hiraldo, F. (1999) Causes and consequences of territory change and breeding dispersal distance in the black kite. *Ecology*, **80,** 1298-1310.

Fuller, R.J. (2012) Habitat quality and habitat occupancy by birds in variable environments. *Birds and habitat: Relationships in changing landscapes* (ed R. J. Fuller), pp. 37-62.

Génot, J.-C. & Van Nieuwenhuyse, D. (2002) *Athene noctua* Little Owl. *BWP Update*, **4,** 35-63.

Gustafsson, L. (1988) Inter- and intraspecific competition for nest holes in a population of the collared flycatcher *Ficedula albicollis*. *Ibis*, **130,** 11-16.

Hanssen, S.A., Hasselquist, D., Folstad, I. & Erikstad, K.E. (2005) Cost of reproduction in a long-lived bird: incubation effort reduces immune function and future reproduction. *Proceedings of the Royal Society of London B: Biological Sciences*, **272,** 1039-1046.

Korpimäki, E. (1988) Effects of territory quality on occupancy, breeding performance and breeding dispersal in Tengmalm's owl. *Journal of Animal Ecology*, **57,** 97-108.

Korpimäki, E. & Hakkarainen, H. (1991) Fluctuating food supply affects the clutch size of Tengmalm's owl independent of laying date. *Oecologia*, **85,** 543-552.

Laundré, J.W., Hernández, L. & Altendorf, K.B. (2001) Wolves, elk, and bison: Reestablishing the "landscape of fear" in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology*, **79,** 1401-1409.

Lima, S.L. (2009) Predators and the breeding bird: Behavioral and reproductive flexibility under the risk of predation. *Biological Reviews*, **84,** 485-513.

Lima, S.L. & Dill, L.M. (1990) Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology*, **68,** 619-640.

Lima, S.L. & Valone, T.J. (1991) Predators and avian community organization: An experiment in a semi-desert grassland. *Oecologia*, **86,** 105-112.

Nur, N. (1984) The consequences of brood size for breeding blue tits I. Adult survival, weight change and the cost of reproduction. *Journal of Animal Ecology*, **53,** 479-496.

Nur, N. (1988) The consequences of brood size for breeding blue tits. III. Measuring the cost of reproduction: Survival, future fecundity, and differential dispersal. *Evolution*, **42,** 351-362.

Nussey, D.H., Wilson, A.J. & Brommer, J.E. (2007) The evolutionary ecology of individual phenotypic plasticity in wild populations. *Journal of Evolutionary Biology*, **20,** 831-844.

Perrig, M. (2015) *Juvenile survival and onset of natal dispersal in little owls (Athene noctua) in relation to nestling food supply*. PhD thesis, University of Zurich, Zurich, Switzerland.

Røskaft, E. (1985) The effect of enlarged brood size on the future reproductive potential of the rook. *Journal of Animal Ecology*, **54,** 255-260.

Schifferli, L., Grüebler, M.U., Meijer, H.A.J., Visser, G.H. & Naef-Daenzer, B. (2014) Barn Swallow Hirundo rustica parents work harder when foraging conditions are good. *Ibis*, **156,** 777-787.

Stearns, S.C. (1989) Trade-offs in life-history evolution. *Functional Ecology*, **3,** 259-268.

Stearns, S.C. (1992) *The evolution of life histories*. Oxford University Press Oxford.

Suhonen, J., Norrdahl, K. & Korpimäki, E. (1994) Avian predation risk modifies breeding bird community on a farmland area. *Ecology*, **75,** 1626-1634.

Thorup, K., Sunde, P., Jacobsen, L.B. & Rahbek, C. (2010) Breeding season food limitation drives population decline of the little owl *Athene noctua* in Denmark. *Ibis*, **152**.

Tuomainen, U. & Candolin, U. (2011) Behavioural responses to human-induced environmental change. *Biological Reviews*, **86,** 640-657.

Van Nieuwenhuyse, D., Génot, J.-C. & Johnson, D.H. (2008) *The little owl: conservation, ecology and behaviour of Athene noctua*. Cambridge University Press, New York, USA.

van Noordwijk, A.J. & de Jong, G. (1986) Acquisition and allocation of resources: Their influence on variation in life history tactics. *The American Naturalist*, **128,** 137-142.

Chapter 1

Reproductive consequences of farmland heterogeneity in little owls (*Athene noctua*)

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Abstract

The amount of high-quality habitat patches, their distribution and the resource accessibility therein play a key role in regulating habitat effects on reproductive success. Heterogeneous habitats offer non-substitutable resources (e.g. nest sites and food) and substitutable resources (e.g. different types of food) in close proximity, thereby facilitating landscape complementation and supplementation. However, it remains poorly understood how spatial resource separation in degraded agricultural landscapes affects reproductive success. To fill this gap, we investigated the relationships between farmland heterogeneity and little owl (*Athene noctua*) reproductive success, including potential indirect effects of the heterogeneity-dependent home-range size on reproduction. Little owl home-ranges were related to field heterogeneity in summer and to structural heterogeneity in winter. Clutch size was correlated with the amount of food-rich habitat close to the nest irrespective of the home-range size, suggesting importance of landscape complementation. Increased time and energy costs linked to large home-ranges did not reduce reproductive success. In contrast, nestling survival was positively correlated with male home-range size, suggesting importance of landscape supplementation. We conclude that decreasing farmland heterogeneity constrains population productivity by the two processes separately: increasing separation of food resources from nest or roost sites results in low landscape complementation and reduction of alternative food resources limits landscape supplementation. Our results suggest that structural heterogeneity affects landscape complementation, whereas the heterogeneity and management of farmland fields affects landscape supplementation. Thus, to what extent a reduction of the heterogeneity within agricultural landscapes results in habitat degradation depends on the ecological processes, which are affected.

Introduction

The amount of high-quality habitat patches, their distribution and the accessibility of resources therein play a key role in regulating habitat effects on reproductive success of animals (Benton et al. 2003). Over the course of a year, animals rely on different types of resources: food, shelter from predators, breeding sites, and winter roosts for thermo-regulation (Orians & Wittenberger 1991; Vickery & Arlettaz 2012; Bock et al. 2013). Not only the availability of different resources, but also their position relative to each other is expected to affect the range use, the linked energy budget, and the reproductive success of individuals. Within the framework of landscape ecology, Dunning et al. (1992) proposed two ecological concepts linked to resource use in fragmented landscapes: populations can benefit from landscape complementation if habitat patches with non-substitutable resources (e.g. nest site and food) are close together, or from landscape supplementation if patches with substitutable resources (e.g. different types of food) occur in close proximity.

In many areas of the world, the intensification of agriculture has resulted in a decline in habitat heterogeneity and biodiversity of farmland habitats, affecting both the amount and distribution of resources (Benton et al. 2003; Tscharntke et al. 2005; Stoate et al. 2009). Increasing levels of habitat heterogeneity in modern agricultural landscapes are suggested to be advantageous if they result in the availability of different types of resources within a small area (Vickery & Arlettaz 2012) The relative importance of specific resources may shift seasonally, as the ecological conditions change (Smith et al. 1978; Douglas et al. 2009; Bock et al. 2013). Therefore, wildlife in farmland habitats has to cope with spatio-temporal variation in resource distribution. Consequently, the importance of spatial ecological processes such as landscape complementation and supplementation might also vary temporally. However, the effect of resource separation in degraded

agricultural landscapes on reproductive success and the underlying mechanisms remain poorly understood.

Landscape heterogeneity may indirectly affect reproduction by causing behavioural home-range size adjustments. If travelling to remote foraging sites within large home-ranges translates into reduced feeding rates, a negative correlation between parental home-range size and reproductive success is expected (Erikstad 1985; Ens et al. 1992; Naef-Daenzer & Keller 1999). In contrast, if home-range size is linked to landscape supplementation and does not entail costs for the brood, access to additional food is expected to result in a positive correlation between parental home-range size and reproductive success.

In this study, we investigate the relationship between landscape heterogeneity in agricultural landscapes and the reproductive success of little owls (*Athene noctua*), a bird species associated with traditional farmlands (Van Nieuwenhuyse et al. 2008). We test four specific predictions to disentangle the direct and indirect effects of landscape heterogeneity: (1) high levels of landscape complementation of nest sites with food resources directly affects reproductive success by providing sufficient food close to the nest. (2) Individuals in inadequately complemented landscapes expand their home-range to supplement their food resources. Depending on the level of landscape supplementation, there is either (3) a negative correlation between parental home-range size and reproductive success, if the time and energy costs of maintaining a large home-range exceed the benefits (cost hypothesis), or (4) a positive correlation between parental home-range size and reproductive success linked to resource supplementation (supplementation hypothesis). Our results give insights into the relative importance of direct and indirect effects of farmland heterogeneity on reproductive success, and the spatial mechanisms underlying this relationship.

Methods

Study species and study area

This study was carried out in the District of Ludwigsburg (Baden-Württemberg, Southern Germany: 48°53′43″N, 9°11′45″E) with a little owl subpopulation consisting of roughly 220 breeding pairs. Due to the disappearance of standard fruit trees and the resulting scarcity of natural breeding sites, little owls often breed in artificial nest boxes. Recent literature shows that orchards and other heterogeneous habitats with a high amount of fallows and field margins are most suitable for the placement of nest boxes (Gottschalk et al. 2011). The little owl population in our study area is an ideal study system to investigate the effects of habitat characteristics on home-range size and reproduction: since density is low and still increasing, it is not expected to affect the home-range size. Furthermore, a review of home-range sizes at different densities of little owls found no correlation between density and home-range size (Van Nieuwenhuyse et al. 2008). Within the study area there is a surplus of nest boxes available (~ 700 nest boxes; H. Keil, unpublished data). The local landscape consists of a mosaic of fields of intensive agriculture interspersed with meadows, orchards, and vineyards (Grüebler et al. 2014)

Reproductive success and food supplementation

During the early breeding season, little owl broods were visited once or twice per week to count the eggs and determine the hatching date (based on the equations of Juillard 1979; and developmental illustrations of Van Nieuwenhuyse et al. 2008). A food supplementation experiment started when the nestlings were approximately 14 days old. Although this experiment was designed for a different study (Perrig et al. 2014), it can provide experimental evidence for the direct effects of food availability on nestling survival. Both control broods without food supplementation (n = 108) and experimental broods (n = 45) were visited every second day for 36 days to closely monitor nestling survival from egg to

fledging. Experimental broods received a total of 480 g additional food per nestling during the nestling and early fledgling period (Perrig et al. 2014). At ringing (nestling age 15-20 days) the nests were checked for unhatched eggs.

Adult characteristics, telemetry, and range use

A total of 139 adult little owls (72 females, 67 males) were captured from 2009 to 2012, either directly within the nest box or using mist-nets set close to the nest box. Body mass and tarsus length were recorded for each individual. Subsequently, they were equipped with very high frequency (VHF) transmitters of own construction (Naef-Daenzer et al. 2005) weighing 6.9 – 7.2 g (approx. 3-5% of a bird's body mass), with an expected life span of 400 days and an operational range of up to 40 km in the field (Bock et al. 2013). The tags were attached with a standard figure-8 harness (Kenward 2001). We located the birds 2–4 times per week using the homing-in technique (Kenward 2001). Per tracking session, two to four fixes at intervals of 5 minutes were collected, yielding a total of 25'654 locations between summer 2009 and summer 2013.

Habitat mapping and variables

Aerial images of ArcGIS 10.0 (ESRI, Redlands, CA, USA) and Google Earth (Version 7.1.2.2041, © Google 2013) were used to map important habitat types within a circle of 180 m radius around each nest (i.e. an area of 10 hectares). Subsequently, the accuracy of the habitat types was verified and corrected in the field. Surface areas covered by cultivated land, orchards, meadows, allotment gardens, vineyards, hedgerows, roads, paths, and human settlement were calculated. This allowed us to compute three biologically relevant variables. First, we calculated the proportion of food-rich habitat (grassland: meadows plus orchards) within the mapped area, hereafter referred to as "amount of food-rich habitat". Since this variable indicates the availability of food-rich

habitat in the close vicinity of the nest site, it is a measure of landscape complementation. As the proportions were always calculated from the same surface area around the nest, they correspond to comparable effective surface areas of food-rich habitat.

Second, as a proxy for field heterogeneity and diversity (see Figure A1.1, Appendix A1), we calculated the mean field size (referred to as “field size”), taking into account adjacent patches of cultivated land with different crops as well as meadows with distinct mowing patterns separately. The field size is also a measure for the distribution of different habitat types: with increasing patch size (higher field size) birds need to pass larger distances across unsuitable matrix to move from one habitat patch to another. Moreover, field size was negatively correlated with the amount of food-rich habitat (Pearson’s $r = -0.37$, $p < 0.001$) and areas with low field size included more edges between different habitat types, which in turn correlates with prey availability and accessibility.

Finally, allotment gardens provide a lot of small structures such as wood stacks, fences or houses for perching. The grass is cut frequently and in winter the snow is cleared, providing high prey accessibility. Already a small area of allotment gardens may supply important resources. Therefore, a binary variable was defined (0 corresponding to mapping areas with less than 10% allotment gardens, 1 to mapping areas with more than 10% allotment gardens) as a proxy for structural richness. Figure A1.2 shows the number of small structures within the two classes (see Appendix A1). Hereafter, this variable is referred to as “structural richness”.

Statistical analyses

Calculation of the home-range sizes

Locations of each individual were split into two seasons, summer (1 April – 30 September) and winter (1 October – 31 March). Thus, the summer season coincides with the breeding season of the little owl up to the point when the nestlings leave the parental home-range

(Van Nieuwenhuyse et al. 2008; Perrig 2015). Fixed kernel density estimates were calculated for all animals with more than 20 telemetry locations using the function kernelUD of the package adehabitatHR (Calenge 2011) in R (R Core Team 2012). Cell size should be considerably lower than the smoothing parameter (h). Therefore, a value of h = 70 m and grid = 500 were used for all home-range size calculations, resulting in cell sizes of mean ± 1 SD = 4.5 ± 2.5 m (range: 0.7 – 15.9 m). We calculated the areas of the 50% and 90% fixed kernel density as a measure of core and full home-range, respectively (Börger et al. 2006). For comparison with previous studies, sizes of minimum convex polygons (95% MCPs) are given in Table A1.1 (See Appendix A1).

Determinants of home-range size

Seasonal and sex-specific relationships between the three habitat characteristics described above and home-range size were analysed by applying linear mixed-effects models. To control for the number of telemetry locations available for each bird, the logarithm of the number of telemetry locations was included as a control variable in all models. Individual ID, nest box ID and year entered the analysis as random factors.

Clutch size, nestling survival and fledgling condition

Linear mixed-effects models were used to investigate the relationships between habitat characteristics and reproductive success. Random intercepts accounted for yearly differences in ecological conditions and interdependence of multiple measurements at the same nest. Variation in clutch size was modelled using linear mixed-effects models with Gaussian error distribution. The three habitat characteristics described above (i.e. amount of food-rich habitat, field size, and structural richness) entered the analysis as fixed focus variables. Nestling survival was modelled in relation to habitat characteristics and food supplementation by applying generalized linear mixed-effects models with binomial error

structure and logit link. The deviation of a fledgling's body mass from the growth curve fitted through all individuals (Perrig et al. 2014; for details see Perrig 2015) was used to investigate the potential effects of habitat characteristics and food supplementation on fledgling condition corrected for age. Since the survival of the parents throughout the breeding season can be crucial for both nestling survival and fledgling condition, we added a binary control variable to these two analyses, stating if one of the parents died during breeding season. As an additional control variable the analyses of nestling survival and fledgling condition included the number of nestlings. Credible intervals (CrI) obtained from the function sim (package arm in R; R Core Team 2012) were used to remove non-significant interactions using backward selection, interactions whose 90% CrI excluded 0 were retained in the models as trends.

Disentangling direct and indirect effects

The above analyses investigate the combined direct (habitat associations) and indirect (habitat-dependent home-range size associations) effects of habitat characteristics on reproductive traits. In order to disentangle direct and indirect effects of habitat heterogeneity on reproductive success, we modelled the target variables described above (clutch size, nestling survival, and fledgling condition) as a function of the three habitat characteristics as well as the home-range sizes of the little owl parents, including the same control variables. Female and male home-ranges were included separately. Since the home-range size depended on the number of telemetry locations collected, we corrected the home-range sizes for the number of points (see Appendix A1 for details). It was not always possible to follow both parents by telemetry. Thus, the inclusion of the home-range sizes reduced the sample size. To test whether changes in effect sizes were due to the inclusion of home-range size or due to the sample size reduction, we used the reduced sample for models including home-range sizes (referred to as "disentangling models") and

without home-range sizes (referred to as “reduced models”). Habitat effects in the disentangling models correspond to direct effects of habitat on reproductive success. Subsequently, we calculated the indirect effects of the different habitat characteristics via home-range size on reproductive success by multiplying the effect sizes of the home-range size in the disentangling models by the effect sizes of the habitat characteristics in the home-range model, calculating standard errors and confidence intervals using error propagation.

Adult age, size and condition

Adults with high intrinsic quality may occupy the best habitats in terms of food abundance and food distribution around the nest. Thus, apparent correlations between habitat quality and reproductive success might be attributable to differences in parental rather than habitat quality. To test for correlations between intrinsic quality and habitat quality, we investigated the relationship between four intrinsic traits of adult little owls (i.e. minimum age, body mass, tarsus length, and as a measure for condition tarsus length corrected body mass) and the three habitat characteristics described above. The analysis of age was simplified by only using the first occurrence of each individual. Age was modelled using a generalized linear model with Poisson error distribution, log link, and the nest box ID as a random factor. Differences in body mass, tarsus length and adult condition were related to sex, amounts of food-rich habitat, field size, and structural richness using linear mixed-effects models, including random intercepts for each individual, nest box, and year.

Scaling and transformation of variables

Continuous variables in the different models were scaled using the same scaling factors to allow comparison of the effect sizes between different models. In addition, the home-range sizes were square-root transformed and logarithmised prior to scaling, to achieve normality

of the model residuals and to enable the calculation of indirect effects. Table A1.2 lists all the scaling factors (see Appendix A1).

Results

Determinants of the home-range size

To determine the relationship between habitat characteristics and home-range size of female and male little owls in the two seasons, 331 home-ranges of 139 individual little owls were calculated: 213 summer- and 118 winter-home-ranges (number of points per home-range: mean = 77.5, range = 21 – 260). In summer, females used a smaller home-range than males (females: mean ± 1 SD: 17.3 ± 10.1 ha; males: 22.0 ± 7.5 ha; Table 1). Both sexes expanded their home-range from summer to winter. However, the home-range expansion of males was less pronounced than that of females, resulting in similar winter home-range sizes for female (28.9 ± 12.8 ha) and male little owls (30.4 ± 11.9 ha; Table 1.1).

Summer home-range size of both sexes was positively related to field size: with an increase of 0.10 ha in field size, little owl home-ranges were extended by 2.17 ha (Fig. 1.1, Table 1.1). Thus, little owls in areas with lower field heterogeneity used a larger home-range. There was no relationship between summer home-range size and the amount of food-rich habitat, even without controlling for field size (Table1.1; effect of food-rich habitat in a model without controlling for field size: -0.017, CrI = -0.165 – 0.128). In winter, there was no relationship between field size and home-range size. Instead, little owls in areas with high structural richness used smaller winter home-ranges than those in areas with low structural richness (19.7 ± 8.6 ha and 24.0 ± 11.9 ha, respectively; Table 1.1).

The analysis of the core home-range size (i.e. the 50% kernel estimate) yielded similar results, except for a missing correlation between summer home-range size and field size. There was a strong correlation between the summer and winter home-range

Table 1.1. Model estimates, standard error and credible interval of the linear mixed-effects model investigating the determinants of home-range size in adult little owls. Home-range size was log-transformed and all variables were scaled. Significant effects are highlighted by bold print, trends are indicated by †.

	Estimate	SE	CrI
Intercept	-1.911	0.427	-2.766 – -1.05
log(Number of locations)	**0.317**	**0.096**	**0.126 – 0.509**
Food-rich habitat	0.029	0.074	-0.118 – 0.179
Field size	**0.202**	**0.088**	**0.026 – 0.373**
Structural richness	0.141	0.218	-0.296 – 0.569
Winter	**1.075**	**0.112**	**0.851 – 1.309**
Males	**0.467**	**0.109**	**0.255 – 0.684**
Field size:Winter	-0.147†	0.079	-0.305 – 0.015
Structural richness:Winter	**-0.680**	**0.204**	**-1.074 – -0.257**
Winter:males	**-0.426**	**0.140**	**-0.708 – -0.157**

Random effects:

Individual: n = 139, explained variance: 0.140

Nest box: n = 87, explained variance: 0.195

Year: n = 5, explained variance: 0.116

Residual variance: 0.343, total number of observations n = 331

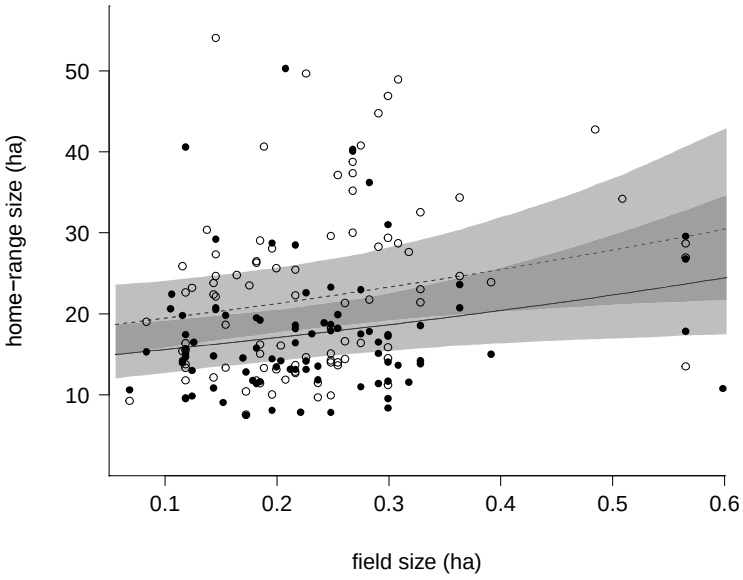

Figure 1.1. Summer home range sizes of female (solid line) and male (dashed line) adult little owls in relation to the field size calculated for a mean amount of food-rich habitat and low structural richness. The grey areas correspond to the 95% credible intervals. Filled and empty circles represent the uncorrected home-range sizes of females (n = 88) and males (n = 89), respectively.

size of males observed over several seasons (Pearson's r = 0.659, CI = 0.447 – 0.801, p < 0.001), whereas the summer and winter home-range sizes of females were only moderately correlated (Pearson's r = 0.444, CI = 0.169 – 0.654, p < 0.01). A post-hoc test showed no relationship between food supplementation and summer home-ranges size (food supplementation and interaction sex:food supplementation: 95% CrI = -0.111 – 0.574 and -0.712 – 0.181, respectively; model with food supplementation only: CrI = -0.159 – 0.360). A second post-hoc test did not reveal any significant relationship between summer home-range size and individual characteristics of male little owls (i.e. age, wing length, tarsus length or body mass), either. There was a trend that female summer home-range size increased with wing length (average home-range increase per mm wing length: 0.22 ha; estimate = 0.057, CrI = -0.005 – 0.094) and decreased with age (average home-range decrease per year of age: 0.345 ha; estimate = -2.764, CrI = -5.737 – 0.131).

Total and direct effects of habitat and home-range size on reproductive success

In the total habitat model, clutch size was positively correlated with the amount of food-rich habitat (Table 1.2). On average, for each additional hectare of food-rich habitat within the 10 ha around the nest, clutch size increased by 0.1 eggs. The total habitat model did not reveal any relationship between the other habitat characteristics and clutch size (Table 1.2). Sample size reduction blurred the total and the direct effect of food-rich habitat on clutch size in the reduced and disentangling model (Table 1.2). However, the inclusion of the female home-range sizes increased the effect size of food-rich habitat compared to the reduced model. There was no correlation between female home-range size and clutch size, either with (Table 1.2) or without controlling for the habitat characteristics (estimate = -0.026, CrI = -0.259 – 0.201). Previous winter home-range size was not significantly correlated with clutch size, although the effect sizes were consistently negative (while controlling for habitat: estimate = -0.223, CrI = -0.526 – 0.069; without controlling for

Table 1.2. Model output of the analysis investigating the determinants of clutch size, nestling survival and fledgling condition. All continuous variables were scaled prior to analysis. Significant effects are highlighted by bold print.

		Total habitat models			Reduced models			Disentangling models		
Model	Parameter	Estimate	SE	CrI	Estimate	SE	CrI	Estimate	SE	CrI
Clutch size	Intercept	-0.092	0.289	-0.667 – 0.474	-0.038	0.386	-0.808 – 0.737	-0.048	0.275	-0.598 – 0.512
	Food-rich habitat	**0.188**	**0.088**	**0.019 – 0.365**	0.114	0.128	-0.142 – 0.375	0.144	0.101	-0.069 – 0.348
	Field size	0.024	0.098	-0.165 – 0.218	0.076	0.128	-0.184 – 0.327	0.061	0.107	-0.162 – 0.275
	Structural richness	0.081	0.225	-0.353 – 0.520	0.185	0.334	-0.487 – 0.850	0.245	0.265	-0.297 – 0.776
	Female home-range size	-	-	-	-	-	-	-0.026	0.115	-0.259 – 0.207
Nestling survival	Intercept	0.682	0.316	0.080 – 1.281	0.962	0.327	0.382 – 1.589	0.773	0.294	0.231 – 1.311
	Food-rich habitat	**0.477**	**0.239**	**0.034 – 0.935**	0.263	0.264	-0.236 – 0.766	0.013	0.245	-0.470 – 0.486
	Field size	0.225	0.261	-0.253 – 0.730	0.092	0.280	-0.455 – 0.641	-0.133	0.270	-0.666 – 0.396
	Structural richness	0.325	0.602	-0.818 – 1.464	0.217	0.663	-1.078 – 1.542	0.438	0.618	-0.748 – 1.638
	Number of nestlings	0.151	0.166	-0.158 – 0.455	-0.040	0.210	-0.408 – 0.329	-0.012	0.177	-0.347 – 0.325
	Parent dead	**-1.953**	**0.476**	**-2.840 – -1.044**	**-2.268**	**1.036**	**-4.253 – -0.286**	**1.050**	**0.477**	**0.109 – 1.969**
	Food supplement.	**1.064**	**0.406**	**0.327 – 1.828**	**0.958**	**0.467**	**0.069 – 1.824**	**-3.445**	**1.265**	**-5.820 – -1.008**
	Food-rich habitat: F.sup.	**-0.785**	**0.377**	**-1.500 – -0.077**	-0.413	0.525	-1.421 – 0.615	-0.134	0.545	-1.199 – 0.947
	F.sup.:Parent dead	**1.946**	**0.796**	**0.406 – 3.434**	1.206	1.324	-1.276 – 3.730	**5.524**	**2.669**	**0.455 – 10.548**
	Female home-range size	-	-	-	-	-	-	-0.154	0.265	-0.661 – 0.366
	Male home-range size	-	-	-	-	-	-	**0.576**	**0.232**	**0.120 – 1.029**

Table 1.2 continued

Model	Parameter	Total habitat models			Reduced models			Disentangling models		
		Estimate	SE	CrI	Estimate	SE	CrI	Estimate	SE	CrI
Fledgling condition	Intercept	-0.163	0.111	-0.390 – 0.054	0.022	0.155	-0.301 – 0.338	-0.024	0.182	-0.410 – 0.361
	Food-rich habitat	0.015	0.092	-0.175 – 0.193	0.052	0.127	-0.209 – 0.311	0.069	0.124	-0.191 – 0.332
	Field size	0.073	0.089	-0.108 – 0.247	-0.089	0.130	-0.357 – 0.177	-0.004	0.142	-0.297 – 0.291
	Structural richness	0.101	0.224	-0.363 – 0.562	-0.006	0.358	-0.761 – 0.716	-0.068	0.357	-0.828 – 0.712
	Number of nestlings	**-0.210**	**0.072**	**-0.36 – -0.063**	**-0.314**	**0.106**	**-0.535 – -0.103**	**-0.326**	**0.105**	**-0.541 – -0.111**
	Parent dead	-0.148	0.184	-0.509 – 0.235	-0.684	0.433	-1.588 – 0.196	**-1.025**	**0.465**	**-1.998 – -0.034**
	Food supplement.	**0.656**	**0.158**	**0.343 – 0.977**	**0.735**	**0.264**	**0.196 – 1.284**	**0.744**	**0.256**	**0.211 – 1.290**
	Female home-range size	-	-	-	-	-	-	-0.132	0.211	-0.570 – 0.322
	Male home-range size	-	-	-	-	-	-	-0.187	0.142	-0.479 – 0.114

Clutch size model: n = 172 observations from 100 nestboxes in 5 years

Reduced clutch size model / clutch size model including home-range size: n = 104 observations of 67 nestboxes in 5 years

Nestling survival model: n = 153 observations from 85 nestboxes

Reduced nestling survival model / nestling survival model including home-range sizes n = 66 observations from 42 nestboxes

Fledgling condition model: 236 observations from 73 broods

Reduced fledgling condition model / fledgling condition model including home-range size: 93 observations from 29 broods

habitat: estimate = -0.212, CrI = -0.503 – 0.083, n = 40). In combination, these results suggest a direct effect of food-rich habitat close to the nest site on clutch size.

In all nestling survival models, the death of a parent reduced nestling survival whereas food supplementation strongly improved survival. Furthermore, a significant interaction between food supplementation and food-rich habitat in the total habitat model revealed a positive correlation between the amount of food-rich habitat and nestling survival in unsupplemented broods (Fig. 1.2, Table 1.2). This correlation was independent from the survival of the parents (Fig. 1.2). Sample size reduction resulted in slightly lower but non-significant effect sizes of food-rich habitat and its interaction with food supplementation. However, the effect of food-rich habitat on nestling survival disappeared completely upon inclusion of the parental home-range size (Table 1.2). Instead, nestling survival was positively correlated with the home-range size of the father, both with (Table 1.2, Fig. 1.3) and without controlling for habitat (estimate = 0.515, CrI = 0.062 – 0.941). In combination, these results suggest that the effect of food-rich habitat on unsupplemented broods in the total habitat model is not based on a direct effect, but rather on an indirect effect associated with home-range size.

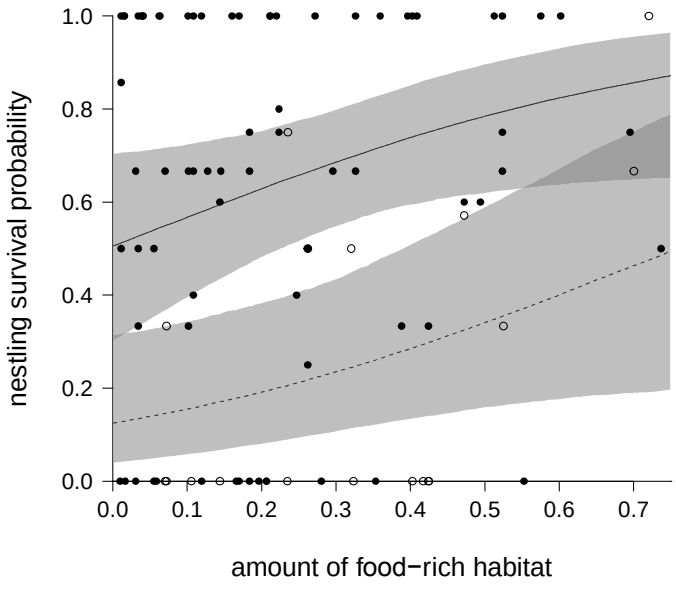

Figure 1.2. Survival probabilities of little owl nestlings in relation to the amount of food-rich habitat close to the nest. The solid line and filled circles indicate broods in which both parents survived, the dashed line and empty circles indicate broods in which at least one adult died or disappeared. Grey surfaces represent 95% credible intervals. n = 108 broods at 76 nest sites.

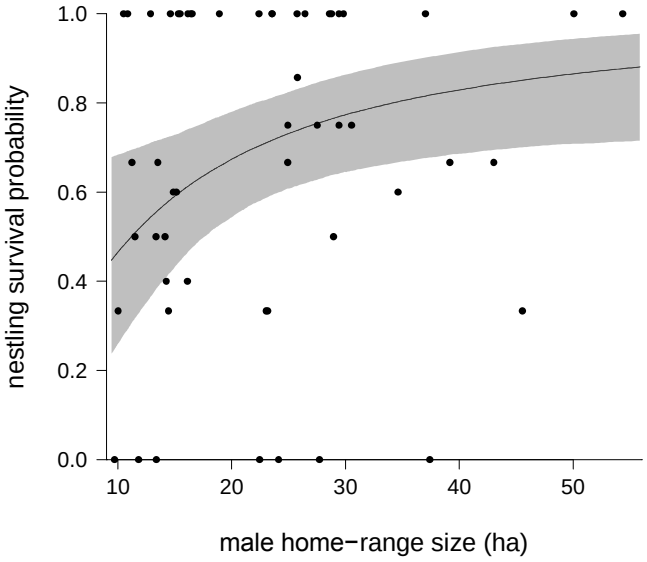

Figure 1.3. Nestling survival in relation to paternal home-range size. The line indicates the model estimate for broods without food supplementation where both parents survived. Filled circles represent the raw data. Grey surfaces represent 95% credible intervals. n = 66 broods at 42 nest sites in 5 years.

Fledgling condition was consistently negatively correlated with brood size (Table 1.2). Similarly, nestlings receiving supplemental food were in significantly better condition at fledging than unsupplemented nestlings in all models (Table 1.2). There were no effects of any habitat characteristics on fledgling condition, neither in the total habitat model nor in the reduced models. Parental home-range size was not significantly correlated with fledgling condition, neither when controlling for the habitat characteristics (Table 1.2) nor without inclusion of these covariates (females: estimate = -0.141, CrI = -0.538 – 0.263; males: estimate = -0.186, CrI = -0.455 – 0.091). The disentangling model revealed an additional negative effect of parental survival on fledgling condition.

Indirect effects of habitat characteristics on reproductive success

We did not find any indirect effects of habitat characteristics affecting clutch size or fledgling condition by modulating home-range size (see Table B1.1, Appendix B1). However, there was a clear trend for a positive indirect effect of field size on nestling survival, indicating that extending home-ranges in monotonous landscapes increased nestling survival (see Table B1.1, Appendix B1).

Adult age, size and condition in habitats of different characteristics

Adults breeding in high quality habitats might be of higher intrinsic quality than individuals breeding in qualitatively poor habitats. Therefore, we tested whether the age, body mass, size or body condition differed between habitats of different quality. Females and males did not differ in their age (Table B1.2, Appendix B1). Furthermore, little owl age did not differ between habitats of the different characteristics measured. Males had a significantly lower body mass than females (152.3 ± 1.8 g and 158.1 ± 1.8 g, respectively). There was a trend that female body mass was positively associated with field size (Table B1.2, Appendix B1). Tarsus length did not differ between the sexes. Male tarsus length was independent from structural richness whereas females in structure-rich areas had significantly longer tarsi. Body condition (body mass corrected for tarsus length) was higher in females. Larger body size of females (measured by the tarsus length) in structure-rich habitats gave rise to a negative relationship between structural richness and female body condition (see Table B1.2, Appendix B1). While female body size was related to the structural richness, none of the parameters of reproductive success were linked to this habitat characteristic (Table 1.2).

Discussion

Our analyses revealed strong effects of habitat characteristics on reproductive success and home-range size of adult little owls, consistent with our predictions (1) and (2). Clutch size was directly affected by the abundance of resources in close vicinity to the nest sites, whereas home-range size of the parents was mainly linked to field heterogeneity in summer and structural heterogeneity in winter. Contrary to prediction (3), we found a positive correlation between nestling survival and the paternal home-range size and an indirect effect of field size on nestling survival, lending support to the supplementation hypothesis (4).

Direct effects of habitat characteristics on reproduction

As expected from recent studies (Hipkiss et al. 2002; Thorup et al. 2010; Perrig et al. 2014), we show that reproduction within our study population is food-limited: experimental supplementation of food to nestlings strongly improved their survival and condition at fledging. In addition, clutch size was positively correlated with the amount of food-rich habitat close to the nest, whereas there was no effect of female home-range size. Although individuals of high intrinsic quality may occupy the best habitats (Sergio et al. 2009; Germain & Arcese 2014), it seems unlikely that the variation in reproductive success found in this study is caused predominantly by variation in individual quality: little owls breeding in areas with high amounts of food-rich habitat did not differ in age, size or condition from those in habitats with low amounts of food-rich habitats. Thus, we found clear correlational and experimental evidence for habitat-driven food limitation of reproduction in little owls.

Effects of habitat characteristics on home-range size

Sunde et al. (2014) recently showed that little owls adjust their habitat selection to weather conditions, most probably due to weather-dependent feeding opportunities in different agricultural fields. Depending on the distribution of different habitats, such range use adjustments to weather may be important determinants of home-range size. In our study, summer home-range size depended on the field size, rather than on the amount of food-rich habitat. However, it has to be considered that habitat mapping only included 180 m around the nest. It is likely that little owls selected patches of food-rich habitat outside of this area, thereby increasing the area of food-rich habitat within their home-range. Furthermore, field size is a measure for the heterogeneity in grassland management and the amount of arable field margins, which determine the accessibility of small rodents

(Shore et al. 2005; Askew et al. 2007; Apolloni 2013), the main nestling food (M.U. Grüebler, unpublished data). Finally, habitat heterogeneity linked to a small field size may provide the necessary diversity for profitable foraging in different weather conditions within a small area.

In winter, little owls select winter roosts with different characteristics than high quality nest sites (Bock et al. 2013), resulting in seasonal changes of the “home base” within home-ranges. Access to winter resources depends on the heterogeneity of structures that provide access to various food types even during periods of frozen ground or snow cover. Accordingly, we show that winter home-range size of adult little owls is linked to structural richness.

Effects of home-range size on reproduction – indirect effects

In altricial birds, effects of food availability on nestling growth and survival always operate via parental provisioning efforts (Naef-Daenzer & Keller 1999; Tremblay et al. 2005; Schifferli et al. 2014). We hypothesized that reproductive success is negatively correlated with home-range size if the costs associated with large distances between food-rich foraging sites and the nest result in decreased allocation of time and energy to reproduction (Ens et al. 1992; Frey-Roos et al. 1995; Hinsley 2000; but see Bruun & Smith 2003). Our results did not support this cost hypothesis: we found no negative correlation between home-range size and reproductive success. In contrast, we found a positive correlation between male home-range size and nestling survival. The indirect effect of field size over home-range size to nestling survival suggests that habitat-driven home-range expansion increased nestling survival. Since the total effect of food-rich habitat on nestling survival disappeared upon the inclusion of the home-range size, it is likely that this effect is based on an indirect effect linked to the home-range size. Although the use of a larger home-range does not seem to entail any costs for the brood, we cannot exclude that

increased costs of foraging in patches far from the nest (Hinsley 2000) are borne by the adults, resulting in reduced adult survival.

Several mechanisms might explain the observed positive correlation: first, in similar habitats, high quality males may be able to defend a larger home-range than their lower quality conspecifics (Carpenter & MacMillen 1976). Hence, the father's intrinsic quality rather than the size of his home-range would cause increased nestling survival. However, we did not find a relationship between individual characteristics of the males and the size of their summer home-range. Second, males may adjust their parental effort to the quality of the female (Burley 1988; Harris & Uller 2009). If so, partners of high quality females would use a larger home-range, thereby improving the survival of their offspring. Again, this was not supported by our data: a post-hoc test did not reveal any positive correlation between male home-range size and individual characteristics of the female (see Table B1.3, Appendix B1). Third, the relationship between home-range size and nestling survival might be caused by the composition and distribution of the habitat outside the mapped area (i.e. farther than 180 m from the nest). If no food-rich habitat is available nearby, either because it is absent over large areas in homogeneous landscapes or because it is occupied by a neighbouring pair, parents do not profit from home-range expansion. Hence, lack of suitable habitat within the surrounding landscape can lead to small home-range sizes and reduced reproductive success (Hinam & St.Clair 2008). A closer examination of small home-ranges with reduced nestling survival supported the third hypothesis: in about 60% of these broods there was either no additional food-rich habitat around the mapped area or the additional food-rich habitat was already occupied by other little owl pairs. Thus, we suggest that home-ranges are expanded if the exploitation of the additional food resources outweighs the cost in terms of energy and time so that the surplus of food can be invested into the current brood.

Heterogeneity at the landscape scale and implications for farmland birds

The results of our study suggest that the recent decrease in farmland heterogeneity linked to intensification of agriculture (Benton et al. 2003; Stoate et al. 2009; Vickery & Arlettaz 2012) constrains population productivity and density by reducing both landscape complementation and landscape supplementation. Landscape complementation is reduced by two processes: first, the removal of structural heterogeneity reduces the availability of high quality nest sites (i.e. tree cavities or nest boxes) within large areas of food-rich habitat (i.e. grasslands). Second, fragmentation increases the separation of these two non-substitutable resources. While the number of nest sites within suitable habitat limits the number of breeding pairs within the landscape, we show that the amount of food-rich habitat surrounding these nest sites affects the reproductive output of individual pairs.

In addition, landscape heterogeneity is correlated with biodiversity (Fahrig et al. 2011). Thus, intensively managed agricultural landscapes characterised by low field heterogeneity offer a low variety of alternative food resources, thereby limiting landscape supplementation. Moreover, the accessibility of prey within food-rich habitats is linked to management heterogeneity (mosaics of different mowing schemes) and availability of perches (Aschwanden et al. 2005; Van Nieuwenhuyse et al. 2008; Apolloni 2013). Breeding home-ranges of resident species are determined by the heterogeneity-dependent level of landscape supplementation, modulated by the constraints of central place foraging. In contrast, winter home-ranges are determined by resource complementation between high quality roost sites and winter food resources. Thus, agricultural habitats with high structural and field heterogeneity, which provide high quality nest and roost sites minimize year-round home-ranges, thereby facilitating high population densities.

Our findings highlight how important it is to know the specific resource requirements of a species for the development of effective conservation plans. In the case of the little owl, we propose two different conservation approaches to increase population productivity: on one hand, conservation efforts should aim to add structural heterogeneity to remaining patches of food-rich habitat within the agricultural landscape, which would increase landscape complementation by providing shelter, roost sites and nest sites. On the other hand, the creation and heterogeneous management of food-rich habitats close to existing nest sites would promote both landscape complementation and supplementation.

Conclusion

This study gives insights into the complex spatial mechanisms underlying the relationships between landscape heterogeneity and productivity in a farmland bird species. Both landscape complementation and landscape supplementation proved to be fitness relevant: high abundance of food resources close to the nest site increases reproductive output whereas low landscape supplementation negatively affects current reproduction. Our results suggest that structural heterogeneity affects landscape complementation, whereas the heterogeneity of farmland fields and their management affect landscape supplementation. Thus, to what extent a reduction of the heterogeneity within agricultural landscapes results in habitat degradation depends on the ecological processes which are affected.

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References

Apolloni, N. (2013) *Landscape use, foraging habitat selection and relationships to food resources in breeding little owls: recognizing the importance of scale for species conservation management*. Thesis, Universität Bern, Bern, Switzerland.

Aschwanden, J., Birrer, S. & Jenni, L. (2005) Are ecological compensation areas attractive hunting sites for common kestrels (Falco tinnunculus) and long-eared owls (Asio otus)? *Journal of Ornithology*, **146,** 279-286.

Askew, N.P., Searle, J.B. & Moore, N.P. (2007) Agri-environment schemes and foraging of barn owls Tyto alba. *Agriculture, Ecosystems & Environment*, **118,** 109-114.

Benton, T.G., Vickery, J.A. & Wilson, J.D. (2003) Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology & Evolution*, **18,** 182-188.

Bock, A., Naef-Daenzer, B., Keil, H., Korner-Nievergelt, F., Perrig, M. & Grüebler, M.U. (2013) Roost site selection by little owls *Athene noctua* in relation to environmental conditions and life-history stages. *Ibis*, **155,** 847-856.

Börger, L., Franconi, N., De Michele, G., Gantz, A., Meschi, F., Manica, A., Lovari, S. & Coulson, T. (2006) Effects of sampling regime on the mean and variance of home range size estimates. *Journal of Animal Ecology*, **75,** 1393-1405.

Bruun, M. & Smith, H.G. (2003) Landscape composition affects habitat use and foraging flight distances in breeding European starlings. *Biological Conservation*, **114,** 179-187.

Burley, N. (1988) The differential-allocation hypothesis: an experimental test. *The American Naturalist*, **132,** 611-628.

Calenge, Clement. (2011) Home range estimation in R: the adehabitatHR package. http://cran.r-project.org/web/packages/adehabitatHR/vignettes/adehabitatHR.pdf.

Carpenter, F.L. & MacMillen, R.E. (1976) Threshold Model of Feeding Territoriality and Test with a Hawaiian Honeycreeper. *Science*, **194,** 639-642.

Douglas, D.J.T., Vickery, J.A. & Benton, T.G. (2009) Improving the value of field margins as foraging habitat for farmland birds. *Journal of Applied Ecology*, **46,** 353-362.

Dunning, J.B., Danielson, B.J. & Pulliam, H.R. (1992) Ecological processes that affect populations in complex landscapes. *Oikos*, **65,** 169-175.

Ens, B.J., Kersten, M., Brenninkmeijer, A. & Hulscher, J.B. (1992) Territory quality, parental effort and reproductive success of oystercatchers (*Haematopus ostralegus*). *Journal of Animal Ecology*, **61,** 703-715.

Erikstad, K.E. (1985) Growth and survival of willow grouse chicks in relation to home range size, brood movements and habitat selection. *Ornis Scandinavica*, **16,** 181-190.

Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, C., Siriwardena, G.M. & Martin, J.L. (2011) Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology Letters*, **14,** 101-112.

Frey-Roos, F., Brodmann, P.A. & Reyer, H.U. (1995) Relationships between food resources, foraging patterns, and reproductive success in the water pipit, *Anthus sp. spinoletta*. *Behavioral Ecology*, **6,** 287-295.

Germain, R.R. & Arcese, P. (2014) Distinguishing individual quality from habitat preference and quality in a territorial passerine. *Ecology*, **95,** 436-445.

Gottschalk, T.K., Ekschmitt, K. & Wolters, V. (2011) Efficient placement of nest boxes for the little owl (*Athene noctua*). *Journal of Raptor Research*, **45,** 1-14.

Grüebler, M.U., Widmer, S., Korner-Nievergelt, F. & Naef-Daenzer, B. (2014) Temperature characteristics of winter roost-sites for birds and mammals: Tree cavities and anthropogenic alternatives. *International Journal of Biometeorology*, **58,** 629-637.

Harris, W.E. & Uller, T. (2009) Reproductive investment when mate quality varies: differential allocation versus reproductive compensation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **364,** 1039-1048.

Hinam, H.L. & St.Clair, C.C. (2008) High levels of habitat loss and fragmentation limit reproductive success by reducing home range size and provisioning rates of Northern saw-whet owls. *Biological Conservation*, **141,** 524-535.

Hinsley, S.A. (2000) The costs of multiple patch use by birds. *Landscape Ecology*, **15,** 765-775.

Hipkiss, T., Hörnfeldt, B., Eklund, U. & Berlin, S. (2002) Year-dependent sex-biased mortality in supplementary-fed Tengmalm's owl nestlings. *Journal of Animal Ecology*, **71,** 693-699.

Juillard, M. (1979) La croissance des jeunes chouettes chevêches, *Athene noctua*, pendant leur séjour au nid. *Nos Oiseaux*, **35,** 113-124.

Kenward, R.E. (2001) *A manual for wildlife radio tagging*. Academic Press, London, UK.

Naef-Daenzer, B., Früh, D., Stalder, M., Wetli, P. & Weise, E. (2005) Miniaturization (0.2 g) and evaluation of attachment techniques of telemetry transmitters. *Journal of Experimental Biology*, **208,** 4063-4068.

Naef-Daenzer, B. & Keller, L.F. (1999) The foraging performance of great and blue tits (Parus major and P. caeruleus) in relation to caterpillar development, and its consequences for nestling growth and fledging weight. *Journal of Animal Ecology*, **68,** 708-718.

Orians, G.H. & Wittenberger, J.F. (1991) Spatial and Temporal Scales in Habitat Selection. *The American Naturalist*, **137,** S29-S49.

Perrig, M. (2015) *Juvenile survival and onset of natal dispersal in little owls (Athene noctua) in relation to nestling food supply*. PhD thesis, University of Zurich, Zurich, Switzerland.

Perrig, M., Grüebler, M.U., Keil, H. & Naef-Daenzer, B. (2014) Experimental food supplementation affects the physical development, behaviour and survival of little owl *Athene noctua* nestlings. *Ibis*, **156,** 755-767.

R Core Team. (2012) R: A language and environment for statistical computing. http://www.R-project.org.

Schifferli, L., Grüebler, M.U., Meijer, H.A.J., Visser, G.H. & Naef-Daenzer, B. (2014) Barn Swallow Hirundo rustica parents work harder when foraging conditions are good. *Ibis*, **156,** 777-787.

Sergio, F., Blas, J., Baos, R., Forero, M.G., Donázar, J.A. & Hiraldo, F. (2009) Short- and long-term consequences of individual and territory quality in a long-lived bird. *Oecologia*, **160,** 507-514.

Shore, R.F., Meek, W.R., Sparks, T.H., Pywell, R.F. & Nowakowski, M. (2005) Will Environmental Stewardship enhance small mammal abundance on intensively managed farmland? *Mammal Review*, **35,** 277-284.

Smith, J.N.M., Grant, P.R., Grant, B.R., Abbott, I.J. & Abbott, L.K. (1978) Seasonal variation in feeding habits of Darwin's ground finches. *Ecology*, **59,** 1137-1150.

Stoate, C., Báldi, A., Beja, P., Boatman, N.D., Herzon, I., van Doorn, A., de Snoo, G.R., Rakosy, L. & Ramwell, C. (2009) Ecological impacts of early 21st century agricultural change in Europe - A review. *Journal of Environmental Management*, **91,** 22-46.

Sunde, P., Thorup, K., Jacobsen, L.B. & Rahbek, C. (2014) Weather conditions drive dynamic habitat selection in a generalist predator. *PLoS ONE*, **9,** e88221.

Thorup, K., Sunde, P., Jacobsen, L.B. & Rahbek, C. (2010) Breeding season food limitation drives population decline of the little owl *Athene noctua* in Denmark. *Ibis*, **152**.

Tremblay, I., Thomas, D., Blondel, J., Perret, P. & Lambrechts, M.M. (2005) The effect of habitat quality on foraging patterns, provisioning rate and nestling growth in Corsican blue tits *Parus caeruleus*. *Ibis*, **147,** 17-24.

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2005) Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. *Ecology Letters*, **8,** 857-874.

Van Nieuwenhuyse, D., Génot, J.-C. & Johnson, D.H. (2008) *The little owl: conservation, ecology and behaviour of Athene noctua*. Cambridge University Press, New York, USA.

Vickery, J. & Arlettaz, R. (2012) The importance of habitat heterogeneity at multiple scales for birds in European agricultural landscapes. *Birds and habitat: relationships in changing landcapes* (ed R. J. Fuller), pp. 177-204. Cambridge University Press, Cambridge, UK.

Appendix A1: Additional methods

Habitat variables and their properties as proxies

Field size was negatively correlated with the Simpson index, a measure of habitat diversity (see Figure A1.1). Thus, a low value for field size corresponds to high habitat diversity. While nest sites with less than 10% allotments within an area of 10 ha had low amounts of small-scale structural elements such as stacks of wood, tree cavities and small houses, structural richness was much higher in areas with >10% allotments (Figure A1.2). Therefore, this variable was used as a proxy for structural richness.

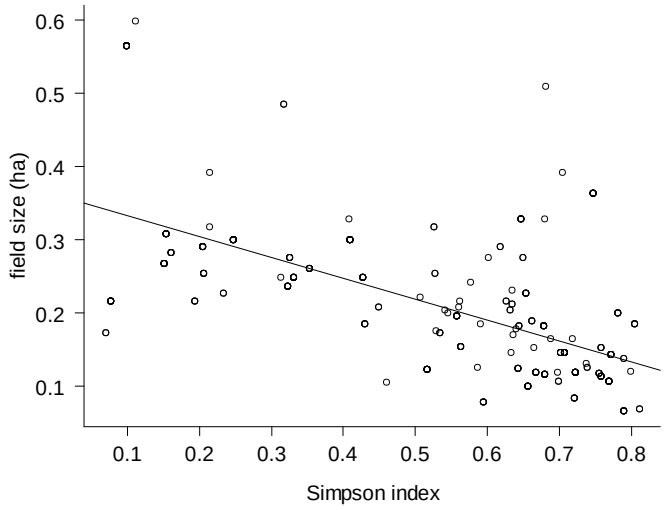

Figure A1.1. Correlation between field size and Simpson index as a proxy for landscape heterogeneity

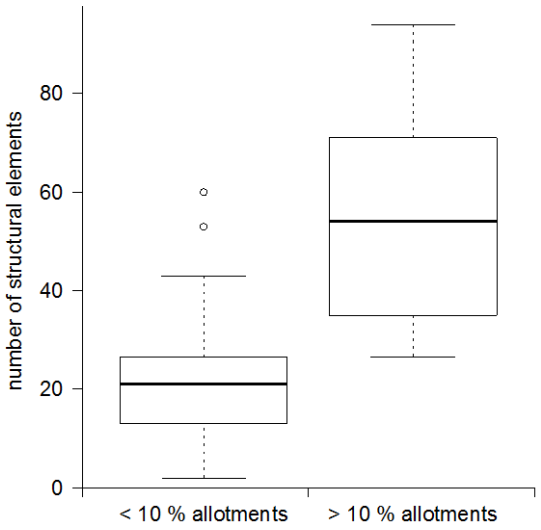

Figure A1.2. Comparison of the number of structural elements in areas with more than 10% and less than 10% allotments.

Table A1.1. Mean, standard error and range of home-range sizes of adult little owls, as estimated by fixed kernel density (KD) and minimum convex polygon (MCP). Numbers after the method indicate the percentage used. n = sample size.

		KD 90			KD 50			MCP 95			n
		Mean	SE	Range	Mean	SE	Range	Mean	SE	Range	
summer	F	17.3	0.7	7.5 – 50.3	4.3	0.2	2.2 – 12.2	13.0	3.0	0.1 – 314.0	106
	M	22.0	1.0	7.6 – 54.1	5.1	0.2	2.3 – 17.9	12.6	3.4	0.2 – 303.9	107
winter	F	28.9	1.7	10.2 – 81.2	7.2	0.5	2.7 – 19.0	21.0	2.7	1.5 – 113.7	55
	M	30.4	1.5	10.5 – 66.8	7.1	0.4	3.0 – 18.8	23.1	2.3	3.3 – 100.5	63

Correction of home-range sizes according to the number of locations

Since the number of telemetry locations was a strong predictor of the home-range size, we corrected the home-ranges with low numbers of locations. Therefore, we wrote an R code, which consecutively selected 20 up to the total number of locations of each animal and calculated the size of the according home-range. This procedure was repeated 100 times for each animal, randomly ordering the locations before each step. From these data we calculated the percental increase of the home-range size with increasing numbers of telemetry locations. This percental increase was first averaged across all the 100 repetitions of each animal and then across all animals, for which the area seemed to reach an asymptote. Since there was seasonal variation in the percental increase, separate curves were calculated for summer and winter, respectively. Figure A1.3 shows the incremental curves for summer (red) and winter home-ranges (blue). According to these curves, the following formulas were used to correct the summer (Eqn. 1) and winter home-range sizes (Eqn. 2) for the number of locations.

$0.9992 + 0.881*(1/x) - 113.5 * (1/x^2) + 1113 * (1/x^3)$ (Eqn. 1)

$1.018 - 1.850*(1/x) - 81.83 * (1/x^2) + 1071 * (1/x^3)$ (Eqn. 2)

While this formula applies very well to numbers of telemetry locations above 20, it cannot be used for lower numbers.

Figure A1.3.

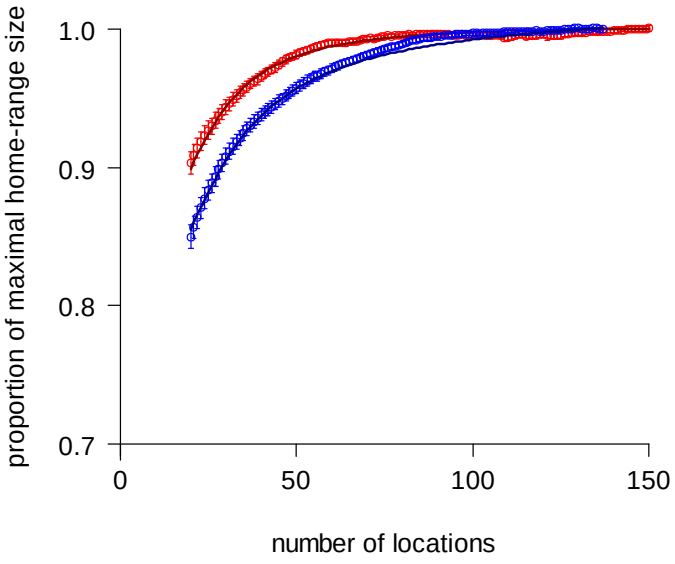

Table A1.2.

Scaling factors of the different variables used in all the models

	Center	Scale
Food-rich habitat	0.263	0.187
Field size	2132	1050
Number of nestlings	3.338	1.087
Log. Home-range size	1.518	0.234

Appendix B1: Additional results

Table B1.1. Comparison of the direct and indirect effects of different habitat characteristics on reproductive success via home-range size. None of the 95% credible or confidence intervals excluded 0. The only case in which the 90% confidence interval excluded 0 is indicated by †.

	Direct effect	CrI	Indirect effect females	CI	Indirect effect males	CI
Clutch size						
Food-rich habitat	0.144	-0.069 – 0.348	0.000	-0.003 – 0.003		
Field size	0.061	-0.162 – 0.275	-0.003	-0.046 – 0.039		
Structural richness	0.245	-0.297 – 0.776	-0.003	-0.035 – 0.029		
Nestling survival						
Food-rich habitat	0.013	-0.470 – 0.486	-0.004	-0.031 – 0.022	0.017	-0.068 – 0.101
Field size	-0.133	-0.666 – 0.396	-0.031	-0.140 – 0.077	0.117†	-0.019 – 0.252
Structural richness	0.438	-0.748 – 1.638	-0.022	-0.120 – 0.077	0.081	-0.173 – 0.335
Residual weight						
Food-rich habitat	0.069	-0.191 – 0.332	-0.004	-0.026 – 0.019	-0.005	-0.034 – 0.023
Field size	-0.004	-0.297 – 0.291	-0.027	-0.114 – 0.060	-0.038	-0.103 – 0.027
Structural richness	-0.068	-0.828 – 0.712	-0.019	-0.100 – 0.063	-0.026	-0.115 – 0.062

Table B1.2. Adult age, size, and condition in habitats of different characteristics. 95% credible intervals of the parameter estimates are given in brackets, bold print indicates credible intervals that do not include 0.

	Age	Body mass	Tarsus	Condition†
Intercept	0.56 (0.36 – 0.75)	158.20 (154.52 – 161.67)	37.13 (36.22 – 38.01)	4.26 (4.13 – 4.39)
Males	-0.06 (-0.33 – 0.20)	**-5.92 (-10.51 – -1.22)**	0.17 (-0.77 – 1.09)	**-0.18 (-0.32 – -0.03)**
Food-rich habitat	-0.04 (-0.20 – 0.11)	1.98 (-0.63 – 4.80)	0.21 (-0.30 – 0.72)	0.02 (-0.06 – 0.10)
Field size	-0.14 (-0.32 – 0.04)	2.35 (-1.58 – 6.30)	0.24 (-0.34 – 0.81)	-0.01 (-0.06 – 0.07)
Structural richness	-0.18 (-0.60 – 0.22)	-0.49 (-7.44 – 6.55)	**2.81 (1.02 – 4.53)**	**-0.33 (-0.60 – -0.06)**
Males:Field size	-	-3.98 (-8.84 – 0.86)	-	-
Males:Structural richness	-	-	**-2.94 (-5.13 – -0.68)**	**0.39 (0.04 – 0.74)**

† Condition was measured as body mass divided by tarsus length to control for body size.

Age model: n = 139 individuals, 85 nestboxes.

Body mass, tarsus and condition models: n = 122 measurements, 76 individuals, 46 nestboxes, 5 years.

Table B1.3. Post-hoc test investigating if male home-range size is linked to the individual characteristics of their mates. Bold print indicates 95% credible intervals excluding 0.

	Estimate	SE	CrI
Intercept	-1.121	1.192	-3.687 – 1.548
log(Number of locations)	0.232	0.287	-0.405 – 0.858
Food-rich habitat	0.106	0.162	-0.243 – 0.453
Field size	**0.575**	**0.194**	**0.159 – 0.989**
Structural richness	0.423	0.435	-0.532 – 1.353
Female wing length	**-0.076**	**0.031**	**-0.144 – -0.010**
Female bodymass	0.092	0.106	-0.145 – 0.332
Female tarsus length	0.029	0.099	-0.185 – 0.246
Female min. age, linear effect	-2.072	2.187	-6.865 – 2.742
Female min. age, quadratic effect	1.733	1.407	-1.406 – 4.894
Female min. age, cubic effect	0.353	1.369	-2.640 – 3.284

n = 69 home-range sizes of males occupying 44 nestboxes during 5 years

Chapter 2

Brood provisioning and reproductive benefits in relation to habitat quality: a food supplementation experiment

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To be submitted

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Abstract

Food availability is a major characteristic of habitat quality, linking habitats with life-history functions such as reproductive performance. Food provisioning of parent birds depends on both the habitat-specific food characteristic and the demands of their young. Since habitat quality and the brood's food intake often are correlated, the underlying mechanisms of adjustments in parental provisioning remain entangled. How the relationship between habitat quality and parental provisioning behaviour affects the quantity of food available to nestlings and the subsequent nestling growth and survival is therefore still incompletely established. By food supplementation of little owl (*Athene noctua*) broods, we experimentally increased the food intake of juveniles raised in two habitats that differ in food availability, thereby disentangling habitat-related effects from brood-related effects on parental provisioning and investigating the effect of extra food on nestling survival. Camera traps recording a series of 10 consecutive images for each parental visit allowed quantifying delivery rates and prey composition by applying a hierarchical multinomial model explicitly accounting for the observation process. Food supplementation caused parents to increase delivery rates and to switch to smaller food items, resulting in similar biomass brought to nestlings. Irrespective of the treatment, parents in low quality habitats fed 2/3 of the biomass compared to those in high quality habitats. Accordingly, we found an increase in nestling survival rates in response to food supplementation in low quality habitats, but not in high quality habitats. Our results show that habitat quality affects the biomass of prey delivered to the brood, whereas the nutritional state of the brood affects prey selection or foraging modes of parents. Reproductive output directly reflects habitat quality in terms of food availability, identifying food as the main resource underlying differential reproduction.

Introduction

Food availability is a major characteristic of habitat quality, linking habitats with life-history functions such as reproductive performance. Limitation of food creates strong trade-offs in the allocation of energy to self-maintenance and reproduction (Martin 1987; Newton 1998). In altricial birds, the impact of habitat-specific food availability on reproduction is modulated by the parental feeding behaviour (Tremblay *et al.* 2003; Byholm & Kekkonen 2008). How the relationship between habitat quality and parental provisioning behaviour affects the quantity of food available to nestlings and the subsequent nestling growth and survival is still incompletely established, in particular in species feeding on a wide variety of prey.

Food supplementation experiments (providing additional food to nestlings) have been applied either to study the adjustments of parental provisioning behaviour to the extra food intake by their nestlings (Hamer *et al.* 1998; Harding *et al.* 2002; Santangeli *et al.* 2012), or to investigate how environmental food constraints contribute to the reproductive performance of wild birds (Wiehn & Korpimäki 1997; Granbom & Smith 2006; Byholm & Kekkonen 2008; Thorup *et al.* 2010; Perrig *et al.* 2014). Although the outcome of experimental food supplementation is expected to differ in relation to the natural environment, only few studies investigated the adjustment of parental provisioning under different environmental conditions. These normally compared years of contrasting food situations (Wiehn & Korpimäki 1997; Karell *et al.* 2009).

In species feeding on a wide variety of prey, parents may not only vary the food delivery rate, but also switch between prey types delivered to the brood (Naef-Daenzer *et al.* 2000; Wilkin *et al.* 2009; Wiebe & Slagsvold 2015). In general, offspring development will be influenced by three components of provisioning: prey type, prey size (i.e. in energy content), and delivery rate (Browning *et al.* 2012). Where prey items largely differ in energy content, foraging or handling efforts, adjustments in parental provisioning might involve

changes in prey selection (Grieco 2002). Unfortunately, accurate quantification of nestling diet remains difficult, because the proportion of identified prey items parents provide to the nestlings is often biased by prey type-specific detection probability (Robinson *et al.* 2015; Francksen *et al.* 2016).

In this study, we aimed at quantifying the food delivery rate, prey composition, delivered biomass, and the consequences for the reproductive output of little owls (*Athene noctua*) in two types of breeding habitats. The two habitats differ in natural food availability (Apolloni 2013). In the poorer habitat little owl home-ranges are larger (Chapter 1), and parental foraging trips during chick rearing are longer and go farther, as compared to food-rich habitats (Staggenborg 2014). In both habitats, we conducted a food supplementation experiment. Food supplementation to the nest enhanced growth rates, body condition and survival of nestlings (Perrig *et al.* 2014). In this study we address the differences between habitats in (1) parental provisioning characteristics in response to the additional food in the nest, and (2) the effect of additional food brought to the nest on nestling survival and thus, reproductive output. A new approach of analysing serial camera trap pictures of feeding visits allowed quantifying prey delivery rates, composition of nestling diet and estimates of delivered biomass, correcting for incomplete prey identification. The results provide insights into the complex mechanisms underlying the relationship between habitat quality and reproductive output and thus, productivity of populations.

Methods

Study area and study species

The little owl (*Athene noctua*) is a cavity breeding owl species of open agricultural habitats (Van Nieuwenhuyse *et al.* 2008). Its diverse diet includes small rodents, insects, earthworms, and birds (Juillard 1984). Our study was carried out in the district of Ludwigsburg (Baden-Württemberg, Germany: 48°53′43″N, 9°11′45″E), a well-populated

region of intensively managed farmlands interspersed with relicts of traditional standard tree orchards of different sizes. The study population was part of a ringing scheme for 25 years and currently consists of roughly 220 breeding pairs (H. Keil, unpublished data), predominantly breeding in nest boxes mounted on fruit trees.

Habitat quality

In the years 2011 and 2012, we selected 56 broods (2011: 25 broods; 2012: 31 broods) in 40 nest boxes located in two distinct habitat types within a gradient of agricultural habitats. First, we selected nest boxes situated on single fruit trees or small tree groups surrounded by large areas of arable fields such as maize, wheat, beet, vegetables and low proportions of permanent grasslands denoted here as “farmland habitats” (2011: 12 broods; 2012: 18 broods). Second, we selected nest boxes situated on orchard trees in large areas of permanent grasslands denoted here as “grassland habitats” (2011: 13 broods; 2012: 13 broods). Recently, we showed that in our study area the availability of an important prey of little owls, the common vole (*Microtus arvalis*), is considerably lower in arable fields than in permanent grasslands (Apolloni 2013). Thus, farmland habitats were assumed to provide poor food resources (low quality habitat) whereas grassland habitats were assumed to provide favourable food resources (high quality habitat). Twenty-one nest boxes within farmland habitats and 19 nest boxes within grassland habitats entered the study. Only nest boxes with unquestionable assignment to the habitat type were used. For details about habitat gradients of broods in the study area and in other German study populations, see Chapter 1 and Staggenborg (2014).

Clutch size and age of nestlings

As in the whole study population, nest boxes were visited monthly from beginning of April to mid-July and checked for occupation. If signs of occupation were present, we checked

the nest boxes weekly until eggs could be recorded and the clutch was full. From the expected hatching date until hatching or brood loss, the nests were visited every three to five days. Using developmental illustrations, we visually estimated the age of nestlings through a spyhole in the nest box without opening the box (Van Nieuwenhuyse *et al.* 2008).

Nestling survival and experimental design

From day 10–14 after fledging onwards, all nest boxes were visited every second day up to fledging at c. 30 days of age. Nestling survival was defined as the survival from eggs to the day 28 after fledging. To experimentally increase the nutritional state of nestlings, parts of the broods were supplemented with dead laboratory mice during these visits: 20 g mouse per nestling during the first 6 visits and 30 g mouse during the rest of the visits were deposited in the nest box. For details about the food supplementation experiment and its effect on nestling development, see Perrig et al. (2014). In each habitat type, 14 broods were experimentally food supplemented, leaving 16 unsupplemented broods in farmland habitats and 12 unsupplemented broods in grassland habitats.

Feeding rates, food items and delivered biomass

At day 8–10 after hatching, a camera trap (Reconyx PC900 Hyperfire camera, RECONYX Inc., Holmen WI, USA) was installed facing the nest box entrance. In addition to the coloured day-time images, an infrared illuminator allowed night-time operation. During subsequent visits, camera traps were controlled and batteries or memory cards were exchanged when required. Although camera traps are increasingly becoming a standard method, we face the problem that food items delivered to nestlings often cannot be identified (Robinson *et al.* 2015). Therefore, we applied a new mark-recapture approach to include detection probability of different food items into the analysis: the cameras were

programmed to take a series of 10 consecutive images at an interval below 1 s when motion was detected by the motion sensor. The observation histories of food items within the 10 consecutive images allowed for quantification of the detection probability. Particularly in windy weather conditions, cameras often took image series due to moving branches or leaves. Therefore, when extracting the data, all image series without visible little owls were excluded. Adults leaving the nest box without food after a feeding event were also recorded by a series of 10 images, but excluded from the data set. Visiting rates were calculated as the number of recorded nest visits by adult little owls per night. For each nest visit, we determined the food item. Nest visits were grouped into six food item types: (1) vertebrates, (2) earthworms, (3) grasshoppers, (4) small insects, (5) no food item (empty bill), and (6) item not visible (unidentified item). Subsequently, we used the series of 10 images to record the observation history of identified food items. Thus, for each of the 10 images, we registered whether the food item (or the empty bill) was visible or not. These encounter histories allowed quantifying the detection probability of each food type. Data of broods aged below day 10 and above day 30 after hatching were excluded because of low sample size. If camera traps were installed before the start of food supplementation, the data were categorized as from unsupplemented broods until food supplementation started.

Statistical analysis

Nestling diet

The composition of diet was analysed using a new approach considering methodological flaws of the camera trap method: a hierarchical multinomial model explicitly including diet-specific detection probabilities. This model was used to correct the number of observed items of the different food types by the probability that a specific food type is detected on an image. Therefore, this model allows for an unbiased estimation of the number of items

of each food type. The model approach also enabled the investigation of relationships between diet composition and predictors such as year, habitat, age of nestlings and food supplementation.

The food type of visit *i* was modelled as a partially observed categorical variable z_i with the following 5 categories: vertebrate, earthworm, grasshopper, small insect, empty bill. The category could only be determined if the item could be identified on at least one of the 10 images. If the item could not be identified on any of the 10 images, the true category of z_i was unknown. The probability that the food item of visit *i* was in category *k* was modelled dependent on year, habitat type and food supplementation including all interactions between food supplementation, habitat and year (8 groups). In addition, we included the age of the nestlings as a covariate and brood identity as a random factor. The latter was included to account for repeated measures of the same brood. The multinomial logit link function was used. To account for different detection probabilities of the food types, we integrated a detection model into the multinomial model. The number of images with identified item for visit *i*, y_i, was modelled as a binomially distributed variable $y_i \sim \text{Binom}(p_i, n_i)$, where p_i is the probability that item *i* is detected on an image and n_i is the number of images made at visit *i* (10 in most cases). The detection probability depended on the food type and a visit-specific random variation, i.e., overdispersion. The latter accounted for temporal autocorrelation within the 10 images of one visit. The logit-link function was used: $\text{logit}(p_i) = \mu[z_i] + \varepsilon_i$, where $\varepsilon_i \sim \text{Norm}(0, \sigma_\varepsilon)$. The notation $\mu[z_i]$ means that for each value (category) of z_i, a separate parameter μ is estimated. The model was fitted in a Bayesian framework using MCMC as implemented in Jags (mcmc-jags.sourceforge.net). So-called "weakly informative" prior distributions were used as recommended by Gelman (2006), i.e. folded t-distribution, T(0,1,2) for σ_ε and σ_b, and Normal distributions with mean of 0 and variance of 25 for the fixed effects. We ran two Markov chains for 200’000 simulations each. The first 10’000 iterations were discarded

and from the remaining values each 40th was used to draw inference about the posterior distribution of the model parameters. Convergence of the chains was assessed visually and by the Rhat-value and effective sample sizes (Brooks & Gelman 1998). The model code is given in the Supplement (Table S2.1).

Visiting rates and nestling survival

We applied generalized linear mixed models (GLMM) within the software R (R Development Core Team 2013) to investigate the factors affecting visiting rates and parental characteristics. Models investigating visiting rates used a Poisson error distribution. Analysis of visiting rate included habitat type and food supplementation as fixed focus variables, as well as year, age and the number of nestlings as fixed control variables. Two-way interactions between year, habitat type and food supplementation were included. However, non-significant interactions as assessed by their 95% credible intervals were deleted from the final model. Brood identity entered the model as a random effect. The model corrected for overdispersion by including an observation-level random effect (Harrison 2014). We used a generalized linear model with binomial error distribution to analyse factors affecting survival of juvenile little owls from the egg stage to fledging (day 28 after hatching). Considering the results of food provisioning, we hypothesised that nestling survival depends on habitat type and food supplementation as these factors were associated with the amount of biomass available at the nest. Thus, we included year as a control explanatory variable, and habitat type, experimental food supplementation and their interaction as focus explanatory variables.

Biomass

For each combination of habitat, food supplement and year, the estimates of the average biomass delivered to the brood per day were based on estimates of visiting rates and the

estimated diet compositions from the hierarchical multinomial model. Information on the biomass of single prey items was not available from the camera traps. Therefore, we extracted values of fresh weight of the main prey species from the literature to roughly estimate the biomass fed to nestlings in the different groups of broods (vertebrates: *Microtus arvalis*, *M. agrestis*, fresh weigth = 25 g: Rychnovska 1993; Meerlo *et al.* 1997; earthworms: adult *Lumbricus terrestris*, fresh weight = 3.7 g: Daniel *et al.* 1996; Kurth & Kier 2014; grasshoppers: *Tettigonia viridissima*, fresh weight = 1.3 g: Antonatos *et al.* 2013; insects [apart from grasshoppers], fresh weight = 0.5 g [average of the values of *Poecilus cupreus*, *Anchonemus dorsalis*, other *Carabidae*]: Desender *et al.* 1994; Arlettaz 1996; Knapp 2012; *Melolontha hippocastani*, *Melolontha melolontha* [*Scarabaeidae*]: Schneider 1980; Wagenhoff *et al.* 2014). Since biomass values of prey items were fixed values, 95% CrI of the biomass reflect the uncertainty of the estimates of visiting rates and diet compositions only, i.e. uncertainty in the assignment of a biomass value to a specific prey item is ignored.

Results

Clutch size

Clutch size was significantly higher in 2012 than in 2011 (B = 0.64, SE = 0.22; P < 0.05) and in grassland habitats compared to farmland habitats (grasslands, unsupplemented: 3.92 ± 0.79 eggs, n =12; farmlands, unsupplemented: 3.25 ± 1.07 eggs, n = 16; B = 0.47, SE = 0.22; P < 0.05). We found no differences in clutch size between supplemented and unsupplemented broods (B = -0.16, SE = 0.22; P = 0.46), reflecting that the assignment to the treatments was unbiased in terms of clutch size.

Diet

Detection probability

The different food items varied considerably in their detection probability. On a single image, the probability to identify a vertebrate was 0.56 (CrI: 0.44 – 0.67), the probability to identify a grasshopper or an earthworm was around 0.2, and the probability to identify small insects was close to zero (Fig. A2.1, Appendix A2). As a result, the probability to detect a food item within 10 images was p = 1 for vertebrates, p = 0.8 (CrI: 0.68 – 0.89) for earthworms, and p = 0.9 (CrI: 0.70 – 0.99) for grasshoppers, but other insects were still very hard to detect (p = 0.01, CrI: 0.01 – 0.01). Interestingly, the probability to identify a nest visit, in which the parent did not bring any food item (classified as “empty bill”) was similar to that of identifying vertebrates and not to that of identifying small insects, which requires a detailed visibility of the bill. This observation suggests that image series with no detectable prey may not represent feeding visits. A closer look at the series without food items revealed that they most probably represent exits from the nest box rather than entries, because the bill was visible at the beginning when birds looked into the camera trap opposite the entrance hole of the box, but not at the end of the series. If so, birds either entered without triggering the camera or were too rapid to be caught by the camera, As a consequence, we counted series of images without food items (“empty bill”) as birds leaving the nest box after the feeding of an unknown item and excluded this category for the estimation of the diet composition and biomass delivered to the brood.

Composition

In total, 12’706 nest visits were recorded. Vertebrates were identified in 6.2%, earthworms in 10.3%, grasshoppers in 2.2% and other insects in 5.2% of the visits. The 24.2% of presumed exits (with unidentified food items during entering) were pooled with the 52.0% of nest visits with completely unidentified food items. We found no differences in the diet

between broods of different sizes. Thus, to simplify the model, we excluded brood size. The diet of little owl parents delivered to their chicks in the nest varied according to the age of nestlings. In the first half of the nestling period, parents brought over 80% insects (Fig. 2.1). In the course of the nestling period, larger food items, i.e. vertebrates, grasshoppers, and earthworms became increasingly important (Fig. 2.1). However, insects were still predominant at the end of the nestling period with c. 50% of the items delivered to unsupplemented broods (Fig. 2.1). Prey composition clearly differed between years (Fig. A2.3, Appendix A2). While in 2011 more grasshoppers were brought to the nest than in 2012, the proportion of earthworms was higher in 2012 than in 2011.

We found differences in the prey composition delivered to nestlings between habitats and between experimental groups (Fig. 2.1). In farmland habitats with low common vole abundance, higher proportions of vertebrates and grasshoppers were delivered compared to grassland habitats where the parents delivered high proportions of other insects. Thus,

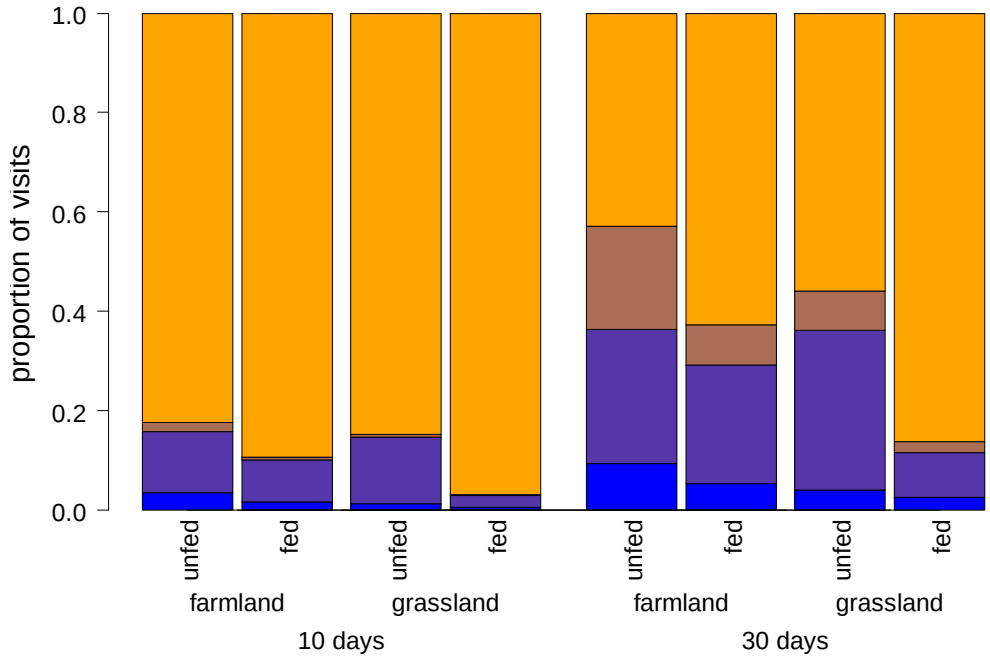

Figure 2.1. Nestling diet composition delivered to supplemented (fed) and unsupplemented (unfed) broods in the two habitats (farmland, grassland). Predicted values for broods in the age of 10 days and 30 days are shown. Blue: vertebrates; violet: earthworms; brown: grasshoppers; orange: small insects.

the age-dependent decline in the proportion of other insects was stronger in farmland broods than in grassland broods. In both habitat types, food supplementation resulted in a considerably higher proportion of other insects in the diet compared to control broods. Consequently, habitats with high natural food availability as well as additional food for the nestlings resulted in an increase in the proportion of other insects and in a decrease in vertebrates in the delivered diet.

Visiting rates

Visiting rates in grassland broods were nearly twice the rates in farmland broods (Fig. 2.2). Thus, although the proportion of vertebrates was lower in grassland broods than in farmland broods, the number of delivered vertebrates was similar. Parents of food supplemented broods in both habitats showed slightly higher visiting rates than parents of control broods (Fig. 2.2). Visiting rates did not differ between years, tended to be higher in broods of larger size, and declined with age of the nestlings (Table 2.1).

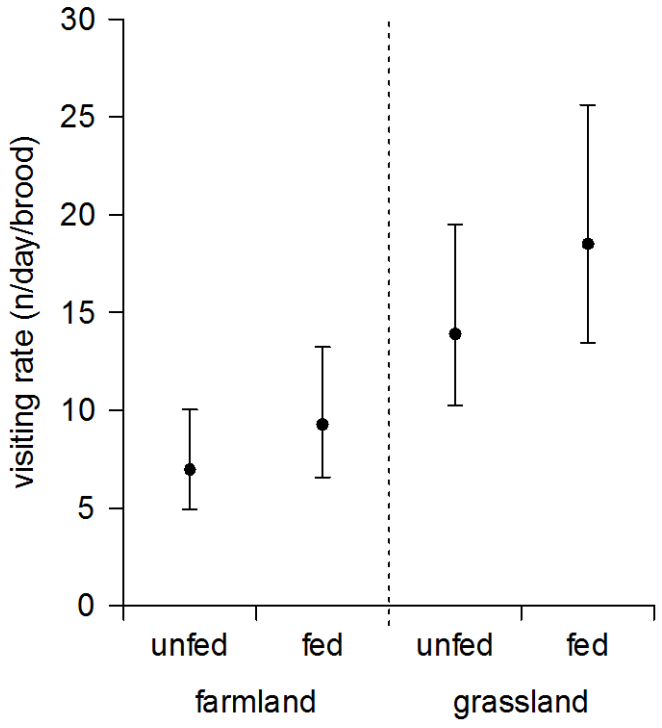

Figure 2.2. Predicted values of daily visiting rates (deliveries/brood) for supplemented (fed) and unsupplemented (unfed) broods in the two habitats (farmland, grassland). Error bars represent 95% credible intervals. N = 56 broods.

Table 2.1. Parameter estimates of factors affecting (a) daily delivery rates (visiting rates) per brood (GLMM, poisson error distribution; N = 789 day of 56 broods; age of the brood as restricted to the period from day 10 to day 30), and (b) nestling survival from the egg stage to fledging (day 28; GLM, binomial error distribution; N = 56 broods)

	(a) Delivery rates		(b) Nestling survival	
Variable	Effect size	CrI	Effect size	CrI lower
Intercept	**1.946**	**1.122 - 2.681**	0.062	-0.623 - 0.730
Year (2012)	0.076	-0.383 - 0.543	-0.103	-0.785 - 0.554
Nestling age	**-0.031**	**-0.042 - -0.020**	--	--
Nestling number	0.178	-0.054 - 0.407	--	--
Habitat (grassland)	**0.691**	**0.272 - 1.153**	**0.962**	**0.140 - 1.779**
Food supplement	**0.286**	**0.006 - 0.555**	**1.929**	**0.951 - 2.940**
Habitat *supplement	--	--	**-1.410**	**-2.781 - -0.049**

Delivery rates: variance component delivery identity: sd = 0.594;

variance component brood identity: 0.806.

Biomass

Although the proportion of vertebrate items in the diet was below 10% in all groups, vertebrates were a main food item in terms of biomass (Fig. 2.3). The absolute delivered vertebrate biomass was similar in broods of both habitats. However, vertebrates represented 48% of the biomass in unsupplemented farmland broods, but only 27% of the biomass in unsupplemented grassland broods. In contrast, total biomass of delivered small insects was considerably lower in farmland broods than in grassland broods, representing 28% and 42% of the total biomass, respectively. Total delivered biomass was higher in grassland broods than in farmland broods (grassland: 34.5 g/day/brood; farmland: 23.5 g/day/brood; Fig. 2.3). This was mainly due to additional biomass delivery in terms of earthworms and small insects in grassland broods. Food supplementation revealed similar adjustments of the feeding behaviour in the two habitats: While total biomass delivered to

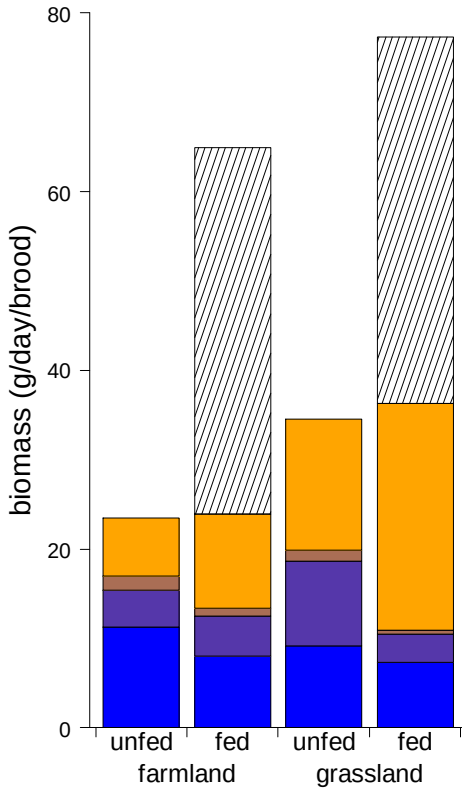

Figure 2.3. Estimates of delivered biomass (g/day/brood) for supplemented (fed) and unsupplemented (unfed) broods in the two habitats (farmland, grassland). Blue: vertebrates; violet: earthworms; brown: grasshoppers; orange: small insects; shaded: amount of food supplemented.

the brood did not change in food supplemented broods, the biomass of small insects considerably increased at the expense of larger prey types (Fig. 2.3).

Survival to fledging

As expected based on the differential amount of biomass provided in grassland and farmland habitats, juvenile survival was lower in farmland habitats than in grassland habitats (Table 2.1; Fig. 2.4). The final survival model included an interaction term between habitat type and food supplementation: In farmland habitats, survival rate to fledging was 0.88 (CrI: 0.74 – 0.95) for food supplemented broods, whereas the rate for unsupplemented broods was 0.51 (CrI: 0.34 – 0.68; Fig. 2.4). In contrast, the survival rate in supplemented grassland broods was 0.83 (CrI: 0.68 – 0.91) compared to 0.74 (CrI: 0.57 – 0.86) in unsupplemented controls.

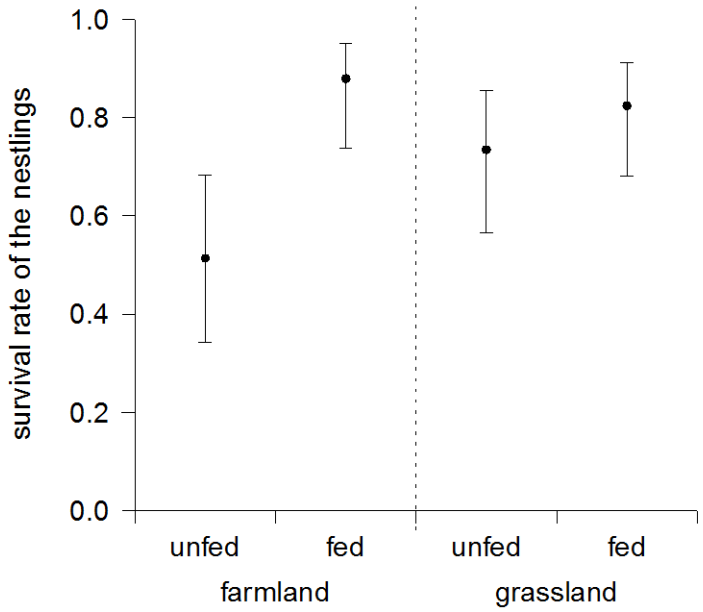

Fig. 2.4. Nestling survival (survival from the egg stage to day 28 from hatching) for supplemented (fed) and unsupplemented (unfed) broods in the two habitats (farmland, grassland). Predicted values for the year 2012 are shown. Error bars represent 95% credibility intervals. N = 56 broods.

DISCUSSION

We have shown that food limitation of the current reproduction differs between habitats with different food availability. By supplementing additional food to the brood we have reduced the effect of food shortage that juveniles may experience during the time in the nest. Food supplementation caused parents to increase delivery rates and to switch to smaller food items, resulting in similar biomass brought to nestlings. These responses were more pronounced in the high quality habitat than in the low quality habitat. However, irrespective of the experiment, parents in low quality habitats delivered only 2/3 of the biomass that parents in high quality habitats delivered. This variation in food input into the nest was associated with a large effect of food supplementation on nestling survival in low quality habitats, but no such effect in high quality habitats. These results suggest that in spite of parental behavioural adjustments to the amount of food available to nestlings, the amount of food delivered depends on the quality of habitats in terms of food availability and translates into habitat-specific survival of offspring to fledging.

Food provisioning represents a period of peak energy expenditure in the annual cycle of altricial birds (Drent & Daan 1980), and therefore strong selection for optimal parental

provisioning decisions is assumed. The finding that owls reduced delivery rates in poor habitats is in line with earlier studies on owls (Hakkarainen *et al.* 1997) and other birds (Naef-Daenzer & Keller 1999; Catry *et al.* 2013). Although parents delivered higher proportions of voles, daily per capita biomass was clearly associated with the habitat-specific delivery rates. Apolloni (2013) showed that in our study area the density of voles, the main prey in the diet in terms of biomass, is considerably lower in farmland than in grassland habitats. Thus, it appears that the differences in delivery rates between the two habitats arise due to increased foraging costs (e.g. higher search time per vole) resulting in a reduced amount of biomass caught per time unit (Naef-Daenzer & Keller 1999; Weimerskirch *et al.* 2000). This is confirmed by the facts that home-range sizes (Chapter 1), flight distances (Staggenborg 2014; Jacobsen *et al.* 2016) and duration of foraging trips during chick rearing (Staggenborg 2014) are considerably larger in poor than in favourable habitats. The results indicate that little owl parents in farmland habitats may be unable to support optimal growth of their nestlings, although they perceive the low nutritional state of their nestlings, because they work at an energetic ceiling (Tinbergen & Verhulst 2000).

The parental response to food supplementation mainly affected the composition of prey items delivered to the brood but not the total biomass. This suggests that behavioural adjustments from poor to favourable habitats involve two separate mechanisms: an increase in delivery rates in response to the higher habitat quality and an increase in the proportion of small prey items in response to the higher amount of food consumed by the nestlings. Food supplementation in little owls is shown to enhance growth and body condition of nestlings (Perrig *et al.* 2014) suggesting a higher nutritional state of nestlings in supplemented broods. Thus parent birds seem to alter prey selection in response to the high nutritional state of their brood.

We see three possible pathways explaining the observed patterns in the composition of prey. First, optimal foraging theory predicts that parents should use the same strategy of

prey size selection within normal limits of provisioning efforts (Wright *et al.* 1998). However, during periods of high demand, selectivity of prey may decline, leading to the delivery of smaller or less nutritious prey items (Wright *et al.* 1998; Grieco 2002; Wiebe & Slagsvold 2015). Our results contradict this mechanism: parents responded to poor food situations in the habitat and in the nest by delivering large rather than small prey items. Second, selectivity for large prey size might increase with high search, handling, and travelling costs, as predicted by the central place foraging theory (Orians & Pearson 1979). Little owls maintain larger home-ranges and make farther foraging trips in farmland than in grassland habitats (Staggenborg 2014; Chapter 1). The selection of large prey during these trips may improve the ratio of effort and benefit. Recent research showed that parents of food supplemented little owl broods reduced the travelling distance compared to parents of unsupplemented control broods (Jacobsen *et al.* 2016). This is in line with the lower prey size in response to food supplementation. However, since vertebrates in grasslands are more abundant close to the nest, we still expect a higher proportion of vertebrates delivered in grasslands than in farmlands rather than vice versa. Third, despite the high profitability of vertebrates during foraging, delivery of vertebrates may entail costs to the parents. Therefore, they may change to a less efficient but less costly foraging mode if nestlings are well fed. Thus, the change in prey types to the extra food in the nest may reflect a behavioural strategy shaping the short-term regulation of self-feeding and feeding the brood. This may also explain that in contrast to existing food supplementation studies (Wiehn & Korpimäki 1997; Hamer *et al.* 1998; Weimerskirch *et al.* 2000; Karell *et al.* 2009; Santangeli *et al.* 2012), little owls increased rather than decreased their delivery rates in response to the additional food, since parental effort might be adjusted by changing prey selection or foraging modes rather than delivery rates.

Experimental food supplementation to the nest increased the proportion of eggs that survived to fledging in low quality habitats but not in high quality habitats. Thus, we show

that in poor habitats the energy flow to the nest is lower than in food-rich habitats, and that this results in lower nestling survival. Detailed analyses of nestling growth and survival revealed that that the amount of food delivered to the nest mainly affects growth rates and survival of last hatched chicks (Perrig *et al.* 2014). These results are in line with a supplementation study in Danish farmlands increasing survival of little owl nestling from 27% to 79% in supplemented broods (Thorup *et al.* 2010). While our supplemented and unsupplemented broods in grasslands showed similar survival rates around 80%, unsupplemented broods in farmlands showed survival rates of 51% and food supplementation in farmlands increased nestling survival to grassland levels. Three major conclusions may be drawn from this result. First, reproduction in the farmland habitats of Denmark is more strongly constrained by food resources than our German study area. This illustrates the large variation in food availability across agricultural landscapes in Europe. Second, the lack of supplementation effect in grassland habitats suggests that in this habitat type the reproductive performance of little owls was close to the maximum. Thus, grassland habitats in our study area represent high quality habitats in terms of food resources. Third, in our study area the agricultural landscapes comprise breeding habitats of variable quality. This means that small scale variation in agricultural landscapes affect reproductive output of little owls suggesting that habitat selection and settlement represent individual behaviours of major fitness relevance. In conclusion, the food supplementation experiments in different habitats quantify the spatial variation in the extent of food limitation on reproductive output in a gradient of agricultural habitats across a species' range. They show that the reproductive output directly reflects habitat quality in terms of availability of food, identifying food as the main resource underlying differential reproduction. Thus, food availability and distribution in agricultural landscapes may be an important factor affecting population productivity and explaining trends in population dynamics of the species.

Methodological issues

This study quantified prey deliveries in relation to habitat quality and experimental food supplementation by using camera traps. This method has some known flaws (Robinson *et al.* 2015). First, the reaction time of the trigger often exceeds the time the bird takes to enter the nest, so that visits are missed. Second, prey items often remain unidentified. We resolved these problems by (1) counting the exits without corresponding entry as nest visits with “unidentified” prey item, and (2) by recording 10 consecutive images allowing for estimation of detection probability for prey of different sizes. By developing a hierarchical multinomial model explicitly accounting for the observation process, we then estimated the proportion of different prey items delivered, corrected for their detection probability. While Robinson et al. (2015) presented an approach to quantify uncertainty in estimates from unidentified food items, our alternative approach additionally considered that food items differ in detectability. Our approach resulted in proportions of vertebrates and invertebrates that are within the range observed in Central Europe (Van Nieuwenhuyse *et al.* 2008). However, delivery rates seem to be low and might be underestimated by camera traps (Staggenborg 2014). We conclude that the application of external camera traps with adequate settings combined with state of the art analyses represents a suitable and easy method to investigate provisioning behaviour with high variation in prey items.

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References

Antonatos, S.A., Emmanuel, N.G. & Fantinou, A.A. (2013) Effect of temperature and species of plant on the consumption of leaves by three species of Orthoptera under laboratory conditions. *European Journal of Entomology*, **110,** 605-610.

Apolloni, N. (2013) *Landscape use, foraging habitat selection and relationship to food resources in breeding little owls: recognizing the importance of scale for species conservation management*. Master thesis, University of Bern,

Arlettaz, R. (1996) Feeding behaviour and foraging strategy of free-living mouse-eared bats, *Myotis myotis* and *Myotis blythii*. *Animal Behaviour*, **51,** 1-11.

Brooks, S. & Gelman, A. (1998) General methods for monitoring convergence of iterative simulations. *Journal of Computational Graphical Statistics*, **7,** 434-455.

Browning, L.E., Young, C.M., Savage, J.L., Russell, D.J.F., Barclay, H., Griffith, S.C. & Russel, A.F. (2012) Carer provisioning rules in an obligate cooperative breeder: prey type, size and delivery rate. *Behavioural Ecology and Sociobiology*, **65,** 1639-1649.

Byholm, P. & Kekkonen, M. (2008) Food regulates reproduction differently in different habitats: experimental evidence in the goshawk. *Ecology*, **89,** 1696-1702.

Catry, I., Franco, A.M.A., Rocha, P., Alcazar, R., Reis, S., Cordeiro, A., Ventim, R., Teodosio, J. & Moreira, F. (2013) Foraging habitat quality constrains effectiveness of artificial nest-site provisioning in reversing population declines in a colonial cavity nester. *PLoS ONE*, **8 (3),** e58320.

Daniel, O., Kohli, L. & Bieri, M. (1996) Weight gain and weight loss of the earthworm *Lumbricus terrestris* L. at different temperatures and body weights. *Soil Biology and Biochemistry*, **28,** 1235-1240.

Desender, K., Dufrêne, M., Loreau, M., Luff, M.L. & Maelfait, J.-P. (1994) Carabid beetles: ecology and evolution. Dordrecht, Springer Science & Business.

Drent, R. & Daan, S. (1980) The prudent parent: energetic adjustment in avian breeding. *Ardea*, **68,** 225-252.

Francksen, R.M., Whittingham, M.J. & Baines, D. (2016) Assessing prey provisioned to Common Buzzard *Buteo buteo* chicks: a comparison of methods. *Bird Study*, **in press**.

Gelman, A. (2006) Prior distributions for variance parameters in hierarchical models. *Bayesian Analysis*, **1,** 515-533.

Granbom, M. & Smith, H.G. (2006) Food limitation during breeding in a heterogeneous landscape. *Auk*, **123,** 97-107.

Grieco, F. (2002) Time constraint on food choice in provisioning blue tits, Parus caeruleus: the relationship between feeding rate and prey size. *Animal Behaviour*, **63,** 517-526.

Hakkarainen, H., Koivunen, V. & Korpimäki, E. (1997) Reproductive success and parental effort of Tengmalm's owls: effects of spatial and temporal variation in habitat quality. *Ecoscience*, **4,** 35-42.

Hamer, K.C., Lynnes, A.S. & Hill, J.K. (1998) Regulation of chick provisioning rate in Manx Shearwaters: experimental evidence and implications for nestling obesity. *Functional Ecology*, **12,** 625-630.

Harding, A.M.A., Van Pelt, T.I., Piatt, J.F. & Kitaysky, A.S. (2002) Reduction of provisioning effort in response to experimental manipulation of chick nutritional status in the Horned Puffin. *Condor*, **104,** 842-847.

Harrison, X.A. (2014) Using observation-level random effects to model overdispersion in count data in ecology and evolution. *PeerJ*, **2,** e616.

Jacobsen, L.B., Chrenkova, M., Sunde, P., Salek, M. & Thorup, K. (2016) Effects of food provisioning and habitat management on spatial behaviour of Little Owls during the breeding season. *Ornis Fennica*, **93,** 121-129.

Karell, P., Pietiäinen, H., Siitari, H., Pihlaja, T., Kontiainen, P. & Brommer, J.E. (2009) Parental allocation of additional food to own health and offspring growth in a variable environment. *Canadian Journal of Zoology*, **87,** 8-19.

Knapp, M. (2012) Preservative fluid and storage conditions alter body mass estimation in a terrestrial insect. *Entomologia Experimentalis et Applicata*, **143,** 185-190.

Kurth, J.A. & Kier, W.M. (2014) Scaling of the hydrostatic skeleton in the earthworm *Lumbricus terrestris*. *Journal of Experimental Biology*, **217,** 1860-1867.

Martin, T.E. (1987) Food as a limit on breeding birds: a life-history perspective. *Annual Review of Ecology and Systematics*, **18,** 453-487.

Meerlo, P., Bolle, L., Visser, G.H., Masman, D. & Daan, S. (1997) Basal metablolic rate in relation to body composition and daily energy expenditure in the field vole, *Microtus agrestis*. *Physiological Zoology*, **70,** 362-369.

Naef-Daenzer, B. & Keller, L.F. (1999) The foraging performance of Great and Blue Tits (*Parus major* and *P. caeruleus*) in relation to caterpillar development and its consequences for nestling growth and fledging weight. *J.Anim.Ecol.*, **68,** 708-718.

Naef-Daenzer, L., Naef-Daenzer, B. & Nager, R. (2000) Prey selection and foraging performance of breeding Great Tits *Parus major* in relation to food availability. *J.Avian Biol*, **31,** 206-214.

Newton, I. (1998) *Population limitation in bird*. Academic Press, San Diego, California, USA.

Orians, G.H. & Pearson, N.E. (1979) On the theory of central place foraging. *Analysis of Ecological Systems* (eds D. J. Horn, R. D. Mitchell & G. R. Stairs), pp. 154-177. The Ohio State University Press, Columbus.

Perrig, M., Grüebler, M.U., Keil, H. & Naef-Daenzer, B. (2014) Experimental food supplementation affects the physical development, behaviou and survival of Little Owl *Athene noctua* nestlings. *Ibis*, **156,** 755-767.

R Development Core Team (2013) *A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Robinson, B.G., Franke, A. & Derocher, A.E. (2015) Estimating nestling diet with cameras: quantifying uncertainty from unidentified food items. *Wildlife Biology*, **21,** 277-282.

Rychnovska, M. (1993) Structure and functioning of seminatural meadows. Amsterdam, Elsevier. Developments in agricultural and managed-forest Ecology 27.

Santangeli, A., Hakkarainen, H., Laaksonen, T. & Korpimäki, E. (2012) Home range size is determined by habitat composition but feeding rate by food availability in male Tengmalm's owls. *Animal Behaviour*, **83,** 1115-1123.

Schneider, P. (1980) Versuche zum Frassverhalten und zur Frassmenge des Maikäfers *Melolontha melolontha*. *Zeitschrift für angewandte Entomologie*, **90,** 141-161.

Staggenborg, J. (2014) *Bewegungs- und Raumnutzungsmuster adulter Steinkäuze (Athene noctua) während der Brutzeit in Abhängigkeit des Habitattyps*. Master thesis, University of Freiburg.

Thorup, K., Sunde, P., Jacobsen, L.B. & Rahbek, C. (2010) Breeding season food limitation drives population decline of the Little Owl *Athene noctua* in Denmark. *Ibis*, **152,** 803-814.

Tinbergen, J.M. & Verhulst, S. (2000) A fixed energetic ceiling to parental effort in the great tit? *Journal of Animal Ecology*, **69,** 323-334.

Tremblay, I., Thomas, D.W., Lambrechts, M.M., Blondel, J. & Perret, P. (2003) Variation in blue tit breeding performance across gradients in habitat richness. *Ecology*, **84,** 3033-3043.

Van Nieuwenhuyse, D., Génot, J.-C. & Johnson, D.H. (2008) *The little owl. Conservation, ecology and behavior of Athene noctua*. Cambridge University Press, Cambridge.

Wagenhoff, E., Blum, R. & Delb, H. (2014) Spring phenology of cockchafers, *Melolontha* spp. (Coleoptera:Scarabeidae), in forests of south-western Germany: results of a 3-year survey on adult emergence, swarming flights, and oogenesis from 2009 to 2011. *Journal of forest science*, **60,** 154-165.

Weimerskirch, H., Prince, P.A. & Zimmermann, L. (2000) Chick provisioning by the Yellow-nosed Albatross Diomedea chlororhynchos: response of foraging effort to experimentally increased costs and demands. *Ibis*, **142,** 103-110.

Wiebe, K.L. & Slagsvold, T. (2015) Foraging trade-offs between prey size, delivery rate and prey type: how does niche breadth and early learning of the foraging niche affect food delivery? *Ethology*, **121,** 1-8.

Wiehn, J. & Korpimäki, E. (1997) Food limitation on brood size: experimental evidence in the eurasian kestrel. *Ecology*, **78,** 2043-2050.

Wilkin, T.A., King, L.E. & Sheldon, B.C. (2009) Habitat quality, nestling diet, and provisioning behaviour in great tit *Parus major*. *Journal of Avian Biology*, **40,** 135-145.

Wright, J., Both, C., Cotton, P.A. & Bryant, D. (1998) Quality vs quantity: energetic and nutritional trade-offs in parental provisioning strategies. *Journal of Animal Ecology*, **67,** 620-634.

Appendix A2: Additional figures

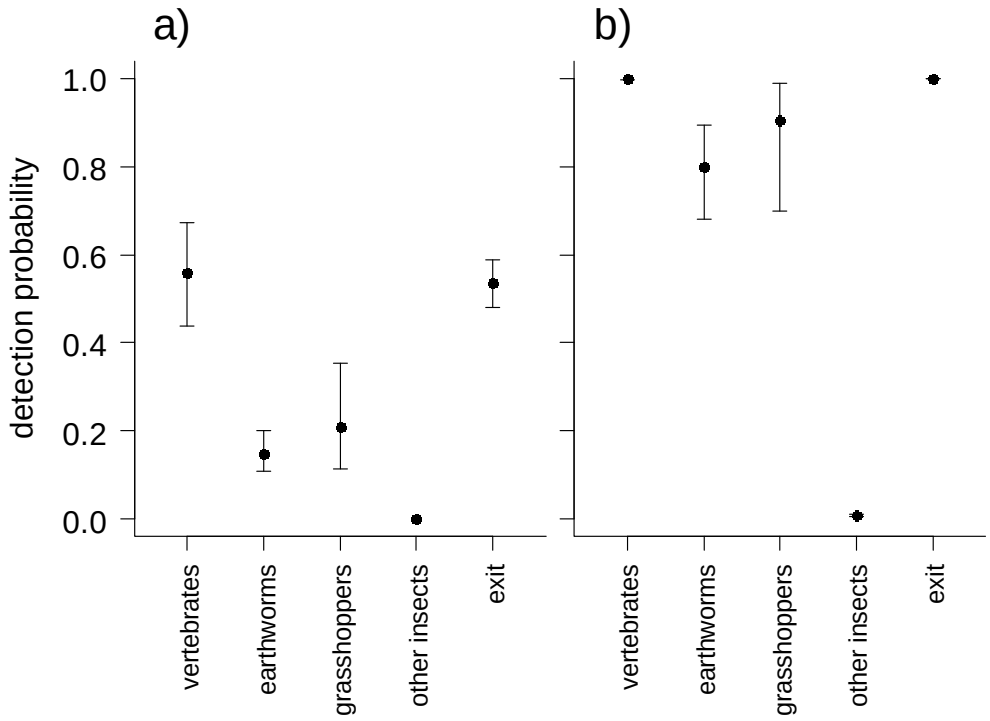

Figure A2.1. Detection probability of the different prey items (a) in one camera trap image, (b) in a series of 10 camera trap images. Nest visits where empty bill was detected showed very high detection probabilities and were classified as exits from the nest box (exit). Error bars represent 95% credibility intervals.

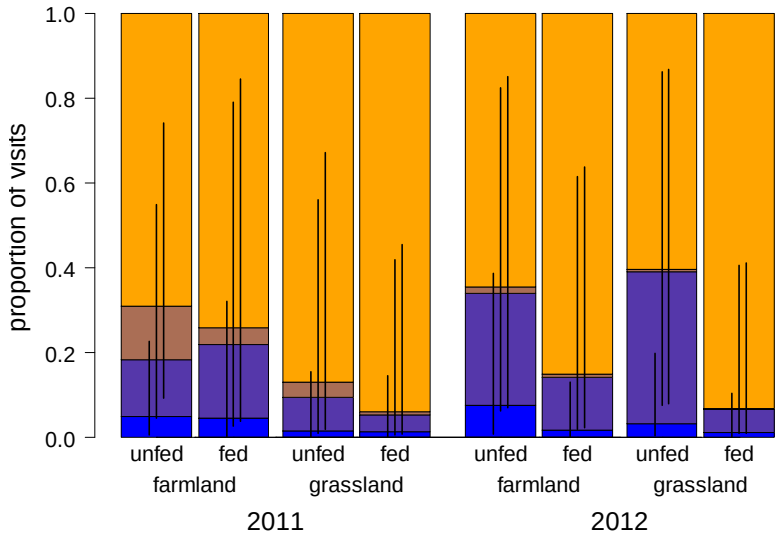

Figure A2.2. Nestling diet composition delivered to supplemented (fed) and unsupplemented (unfed) broods in the two habitats (farmland, grassland). Predicted values for the mean age (day 19) in the two year are shown. Blue: vertebrates; violet: earthworms; brown: grasshoppers; orange: small insects. Error bars represent 95% credibility intervals.

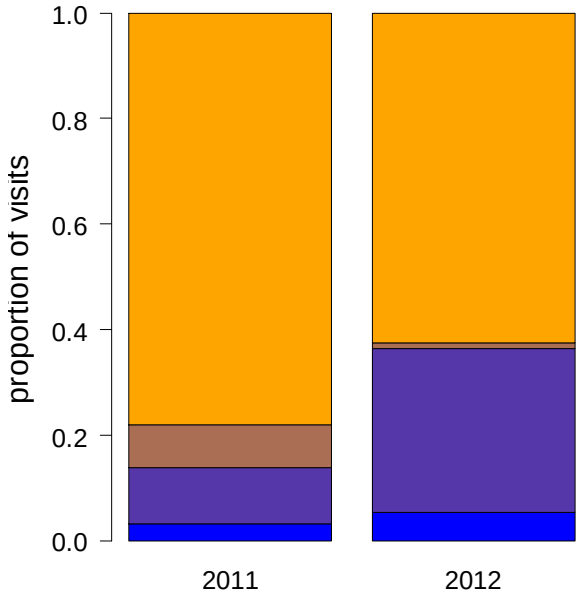

Figure A2.3. Predicted values of nestling diet composition delivered to unsupplemented broods (mean value of the two habitats) in the two study years. Age was set to the mean value. Blue: vertebrates; violet: earthworms; brown: grasshoppers; orange: small insects.

Supplement 2: Jags-Code of the hierarchical multinomial camera trap model

Table S2.1. Notation of data and parameters

Notation	Description
Data	
n	number of feeding events (value 12706)
ncat	number of categories (value 4)
group	indicator of group of brood: 1 = Farmland not fed 2011, 2 = Farmland not fed 2012, 3= Farmland fed 2011, 4 = Farmland fed 2012, 5 = Grassland not fed 2011, 6 = Grassland not fed 2012, 7 = Grassland fed 2011, 8 = Grassland fed 2012; vector of length 12706
agejuv	age of nestlings, z-transformed (so that the mean is zero and the standard deviation 1); vector of length 12706
broodid	indicator of brood, vector of length 12706
nbrood	number of broods (value 56)
nocc	number of pictures made by the camera of each feeding event; vector of length 12706
ysum	number of pictures on which the item is visible among the number of pictures made by the camera; vector of length 12706
Partially observed variables	
z	Item type delivered to the brood at a feeding event: 1 = vertebrate, 2 = worm, 3 = grasshopper, 4 = other insect. When the item was not visible on any of the pictures made for one feeding event, this variable was missing (NA).
Parameters	
beta	model coefficients (fixed effects) of the multinomial linear predictor; 9 x ncat matrix; the first 8 rows contain the means of the linear predictor for each group and food item type, the 9th row corresponds to the effect of nestling age on item type
broodeff	brood-specific random deviation from the mean of the linear predictor (brood-specific random effects)
taubrood	precision (=1/variance) of the brood-specific random effects
e	probability that a food item is detected and identified by one picture of the camera during a specific event; vector of length 12706
e0	item type-specific probability that the item is detected and identified on one picture of the camera (logit-transformed)
epsilon	event-specific deviation of the detection probability from the item-specific detection probability (in the logit-scale); this parameter account for overdispersion
tauepsilon	precision (=1/variance) of the event-specific deviation of the detection probability
Indices	
i	feeding event, total 12706
k	food item types, total 4
u	model coefficient (fixed effects), total 9
j	brood, total 53

Jags code of the model

```
model {
# likelihood
for(i in 1:n){
  z[i]~dcat(p[i, 1:ncat])
    for(k in 1:ncat){
      pz[i,k] <- beta[group[i],k] + beta[9,k]*agejuv[i] + broodeff[broodid[i], k]
      exppz[i,k] <- min(exp(pz[i,k]), 1000)
      p[i,k] <- exppz[i,k]/sum(exppz[i,1:ncat])
      } # close k
  ysum[i]~dbinom(e[i], nocc[i])
  logit(e[i]) <- e0[z[i]] + epsilon[i]
  epsilon[i] ~ dnorm(0, tauepsilon)
} # close i

# priors
for(u in 1:9){
  beta[u,1] <- 0
} # close u
for(j in 1:nbrood){
  broodeff[j,1] <- 0
} # close j
for(k in 2:ncat){
  for(j in 1:nbrood){
    broodeff[j,k]~dnorm(0, taubrood)
  } # close j
  for(u in 1:9){
    beta[u,k]~dnorm(0,0.44)
  } # close u
} # close k
for(k in 1:ncat){
  e0[k]~dnorm(0,0.44)
} # close k

tauepsilon~dt(0,1,1)T(0,)
taubrood~dt(0,1,1)T(0,)
} # close model
```

Chapter 3

Food supply during the breeding season affects the survival of adult little owls (*Athene noctua*) over the whole annual cycle

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To be submitted

Keywords: Carry-over effects, costs of reproduction, food supplementation, multi-state model, telemetry

Abstract

One of the most important life-history trade-offs faced by adult animals is the allocation of energy among reproduction and self-maintenance during the breeding season. Although reproduction is expected to be costly, empirical evidence for the survival costs of reproduction in relation to food supply is scarce. In this study, we investigated the survival costs of reproduction for adult little owls (*Athene noctua*) by providing supplementary food to the nestlings and thereby reducing parental effort. Radio-tracking and Bayesian multi-state modelling based on marked recapture and dead recovery were applied to estimate survival rates of adult little owls in different periods of the annual cycle as a function of food supplementation and natural habitat characteristics while controlling for individual characteristics. Food supplementation during the breeding season increased the survival of both sexes, not only during the breeding season but also during winter and the rest of the year. A significant interaction between the amount of food-rich habitat surrounding the nest and food supplementation suggests that, during the breeding season, parents in low quality habitats did not profit from food supplementation. We suggest that these results reflect differential parental investment in poor compared to favourable habitats. In addition to regulating population productivity, breeding season food supply also affects the demographic structure and the turn-over of populations by regulating adult survival. Our results contribute to the understanding of the mechanisms which link habitat heterogeneity with individual survival and demographic rates.

Introduction

One of the most important life-history trade-offs faced by adult animals is the allocation of energy among reproduction and self-maintenance during the breeding season (Stearns 1989; Roff 1993; Martin 1995; Ghalambor & Martin 2001). Food availability within the habitat can strongly affect the outcome of this trade-off (Martin 1987). In many species, low food supply during the breeding season reduces the survival and condition of the young (Sundell *et al.* 2004; Schifferli *et al.* 2014; Perrig *et al.* 2014), but there is growing evidence that the parents also bear some of the costs (Oro & Furness 2002; Davis *et al.* 2005; Kitaysky *et al.* 2010). Depending on the mechanisms, which link increased parental efforts to a reduction in survival or future reproduction, these costs may occur during the current reproductive attempt (proximate effects; Sheldon & Verhulst 1996; Descamps *et al.* 2009; Low *et al.* 2010) or carry over to later life history stages (ultimate effects; Nilsson & Svensson 1996; Alonso-Alvarez *et al.* 2004; Reichert *et al.* 2014). However, the direct relationship between habitat-dependent parental effort and future fitness consequences remains poorly investigated.

Fitness costs of reproduction may affect future fecundity (Hanssen *et al.* 2005), timing of breeding (Brommer *et al.* 2004), and adult survival (Daan *et al.* 1996). However, these costs may be confounded by individual quality if some individuals are consistently better at acquiring resources, allowing them to allocate more resources to several life-history traits (van Noordwijk & de Jong 1986; Hamel *et al.* 2009). Experimental approaches such as brood size manipulations or food supplementation are necessary to disentangle the effects of ecological conditions and individual quality. Both these experimental treatments cause adjustments in parental effort while leaving the environmental conditions unchanged (De Steven 1980; Hegner & Wingfield 1987; Martins & Wright 1993; Santangeli *et al.* 2012). Experimental food supplementation positively affects offspring survival and condition (Dhindsa & Boag 1990; Wiehn & Korpimäki 1997;

Hipkiss *et al.* 2002; Brommer *et al.* 2004; Perrig *et al.* 2014). At the same time, it decreases the delivery rates of parents as a response to the reduced needs of their offspring, thereby reducing parental work load (Wiehn & Korpimäki 1997; Brommer *et al.* 2004; Eldegard & Sonerud 2010; Santangeli *et al.* 2012). However, to our knowledge, no previous experimental study has addressed the causal chain ranging from natural food abundance via parental reproductive effort to post-reproductive survival.

While previous experimental studies have shown that productivity of little owls (*Athene noctua*) is limited by the food supply during the breeding season (Thorup *et al.* 2010; Perrig *et al.* 2014), it remained unclear whether the food limitation during the breeding season also affects adult survival. Therefore, we studied the effects of experimental food supplementation on the survival of adult little owls, while taking into account habitat characteristics linked to natural food abundance. Radio-tracking data with a high temporal resolution allowed us to investigate whether there are survival costs of reproduction during the breeding season, or whether the costs carry-over to subsequent periods of the year. Based on the assumption that food supplementation reduces the work load of parents, we predicted that food supplementation increases parental survival, and that experimental treatment interacts with the natural food availability. Our experimental results give insights into the mechanisms shaping the trade-off between current reproduction and survival in habitats of different quality, and thus, provide evidence for considerable costs of reproduction incurred by breeding birds.

Methods

Study species and study area

The little owl is a small nocturnal owl living in open areas of Europe (Van Nieuwenhuyse *et al.* 2008). Due to its small size it is susceptible to several larger predators (Schönn *et al.* 1991). Little owl populations have been declining across Western and Central Europe

within the last couple of decades (Šálek & Schröpfer 2008; Zmihorski *et al.* 2009; Le Gouar *et al.* 2010; Thorup *et al.* 2010). Within our study site, the District of Ludwigsburg (Baden-Württemberg, Southern Germany: 48°53′43″N, 9°11′45″E), the placement of artificial nest boxes has led to a population increase from eight known breeding pairs in 1988 to currently 220 (H. Keil, unpublished data). Individual breeding pairs occupy areas of varying habitat characteristics (see Chapter 1).

Tagging procedure

From summer 2009 to summer 2012 a total of 125 individual adult little owls (67 females, 58 males) were caught, either using mist nets or directly in the nest box. Many of those birds were already ringed as nestlings, providing us with information of their exact age. For first-time captures, a minimal age of one year was assumed. After capture, the body mass of each little owl was measured and it was equipped with a very high frequency (VHF) transmitter of own construction (Naef-Daenzer *et al.* 2005; Bock *et al.* 2013) weighing 6.9–7.2 g (i.e. 4–5% of a bird's body mass). These transmitters have an operational range of up to 40 km in the field and an expected life span of 400 days. Birds that survived until the subsequent breeding season were recaptured and transmitters were replaced. In summer 2013, all surviving adults were recaptured to remove the remaining transmitters.

Radio tracking

During 2–4 visits per week, each bird was located twice at an interval of 5 minutes by homing in using a 3-element Yagi antenna and a handheld receiver (Kenward 2001). This allowed us to determine whether the individual was active or inactive. In case of extended inactivity, the little owl was located during the day to check for mortality. Thanks to the reach of the transmitters, even remains of animals buried by red foxes (*Vulpes vulpes*) could be recovered (Naef-Daenzer *et al.* 2016). All recapture data was summarized into

biweekly recapture histories, indicating if an individual was observed alive (1), recovered dead (2), or neither observed alive nor recovered (3). In addition, summer and winter home-range sizes of most individuals were available from Chapter 1. For the remaining individuals, we predicted home-range sizes using the home-range size model of Chapter 1. Furthermore, home-range sizes were corrected for the number of telemetry fixes (see Appendix A1, Chapter 1).

Food supplementation experiment

Food supplementation started when the nestlings were approximately 14 days old. Both control broods (n = 66) and experimental broods (n = 38) were visited every second day for 36 days. Experimental broods received 20 g of dead laboratory mice per nestling during the first six visits and 30 g during the subsequent 12 visits, amounting to a total of 480 g additional food per nestling (Perrig *et al.* 2014).

Habitat classification

Important habitat types within a circle of 180 m radius around each nest (i.e. an area of 10 hectares) were mapped using aerial images of ArcGIS 10.0 (ESRI, Redlands, CA, USA) and Google Earth (Version 7.1.2.2041, © Google 2013). Subsequently, the accuracy of the habitat types was verified in the field and corrected if necessary. Surface areas covered by cultivated land, orchards, meadows, allotment gardens, vineyards, hedgerows, roads, paths, and human settlement were calculated. From these data we computed three different habitat characteristics. First, we calculated the proportion of meadows and orchards within the mapped area as a proxy for the food abundance close to the nest, hereafter referred to as “amount of food-rich habitat”. Second, we calculated the mean field size (referred to as “field size”), which is a measure for field heterogeneity and diversity. Finally, allotment gardens provide a lot of small structures such as wood stacks,

old trees with natural cavities, fences or houses for perching. Due to the high accessibility of prey and the supply of shelter from predators, already a small area of allotment gardens may be beneficial for survival. Therefore, a binary variable was defined (0 corresponding to mapping areas with less than 10% allotment gardens, 1 to mapping areas with more than 10% allotment gardens), referred to as “structural richness”. See methods section of Chapter 1 for a more detailed description of the three habitat variables.

Statistical procedures

Scaling of the variables

Field size, amount of food-rich habitat, home-range size, and clutch size were scaled to a mean of zero and a standard deviation of one prior to the analyses. Due to seasonal and sex-specific home-range size variation, home-range size was scaled for females and males as wells as for summer and winter separately. In addition, clutch size was scaled separately for each year.

Modelling survival

A mix between marked recapture and dead recovery (Lebreton *et al.* 1999; Kéry & Schaub 2012) was used to model survival in relation to different individual and environmental characteristics. This multi-state model accounts for the detection probability of individuals with unknown fate (Lebreton *et al.* 1999). Since transmitter failure was low, we only included three true states in the model: 1 for live animals, 2 for recently dead animals, whose transmitter or remains were recovered, and 3 for dead individuals that have been dead for a while, some of which have not been recovered (absorbing state).

Model selection and development of the final model

During the pilot study in 2009, development of transmitters was not finished and consequently the rate of transmitter loss was higher. Therefore we included two different intercepts for detection rate, one for 2009 and one for the other years (Naef-Daenzer & Grüebler 2014). Moreover, we included a sex effect on detection probability. As an additional nuisance parameter, we included a constant recovery probability for all intervals.

Previous analyses of the survival of adult little owls identified two periods of reduced survival, the breeding season and winter (Glue 1973; Exo & Hennes 1980; Thorup *et al.* 2013). Accordingly, we defined three focus periods to test if nestling food supplementation affects adult survival during the breeding season or during subsequent time periods. First, we defined the breeding season as the start of incubation at the beginning of May until the time when juveniles leave the parental home-range at the end of August. Second, according to the findings of Exo & Hennes (1980), we defined “winter” as the two biweekly intervals from mid-January to mid-February. Third, all remaining biweekly intervals, i.e. September to mid-January and mid-February to April, were combined as the “rest of the year”.

In a second step, we created a full model including all focus variables (sex, food supplementation, the three habitat characteristics, summer and winter home-range sizes, and clutch size) as well as the control variables (age, age^2, and body mass). We included interactions between sex and all other variables as well as between food supplementation and the three habitat characteristics investigated. To test if the effects of the focus variables differed between the three time periods, we calculated the effects for each of the three periods separately. During a first reduction step, covariates whose effects did not differ significantly between the three time periods were reduced overall effects for all periods. Moreover, all three-way interactions with an f-value (i.e. proportion of posterior distribution on the same side of zero as the mean) below 0.9 were removed. In the

absence of three-way interactions, all two-way interactions with f < 0.9 were removed. A second reduction step eliminated all remaining interactions with f < 0.9. Due to the a priori identification of the variables of interest, all main effects were kept in the final model (Homberger *et al.* 2014). All models were run in JAGS (Plummer 2003) controlled by the R package jagsUI (Kellner 2015) in R version 3.2.3 (R Core Team 2015). Three chains were run for 100'000 iterations with a burn in of 50'000 and no thinning. Convergence of the Markov chains was checked with Brooks-Rubin-Gelman diagnostics (Brooks & Gelman 1998). For the code of the final survival model see Supplement S3, for the output of the full model and the model after the first reduction step see Tables A3.1 and A3.2, Appendix A3). Unless stated otherwise, the results are given as posterior means with the 95% credible interval (CrI) in square brackets, calculated for mean values of the other variables and age = 3 years.

Results

Detection and recovery probability

Detection probability was lower in 2009 than in the other years. In addition, female detection probability was lower than male detection probability (posterior mean [CrI] for 2009: females: 0.76 [0.70–0.82], males: 0.82 [0.75–0.87]; for the rest of the years: females: 0.91 [0.90–0.92], males: 0.94 [0.92–0.95]). The recovery rate was 0.65 [0.63–0.67]. Thus, the transmitter or the remains of 65% of the birds were recovered after their deaths.

Seasonal and sex-specific differences in survival

Survival probability differed significantly between the time periods (Fig. 3.1). Female and male survival rates were similar during winter (January / February), whereas the female survival rate was lower during the breeding season (May – August; f = 0.98) and in the rest

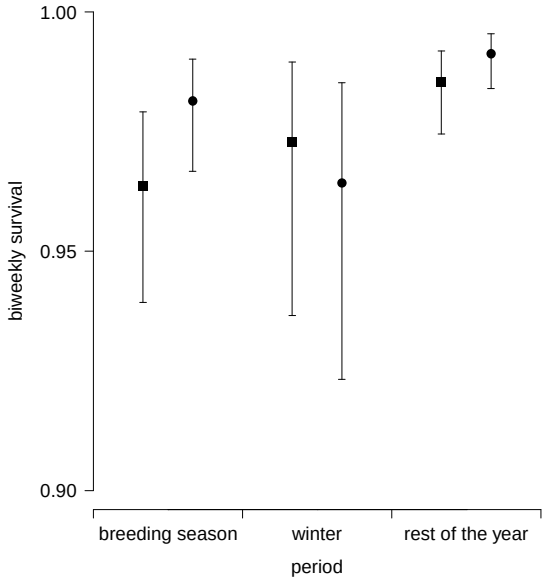

Figure 3.1. Biweekly survival rates of female (squares) and male little owls (circles) in different periods throughout the year. Error bars represent the 95% CrI.

of the year (September – December and February – April; f = 0.95, Fig. 3.1). Although there were some inter-annual differences, as indicated by the large credible intervals, year-specific winter survival rates did not improve the model and therefore were not included the final model. During most of the year both female and male survival was high (biweekly survival rate of females: 0.985 [0.974 – 0.992], males: 0.991 [0.984 – 0.995]). Over the course of the breeding season, survival of females and males was reduced (0.964 [0.939 – 0.979] and 0.981 [0.967 – 0.990], respectively). Finally, there was an additional peak in little owl mortality during winter (females: 0.973 [0.937 – 0.990], males: 0.964 [0.923 – 0.985]; Fig. 3.1).

Food supplementation and habitat characteristics

In general, parents of supplemented broods had higher survival rates than parents of un-supplemented broods, irrespective of the period (Table 3.1). We found two exceptions from this pattern. First, we found a significant interaction between period, food supplementation, and the amount of food-rich habitat. This indicates that, during the breeding season, survival did not differ between supplemented and un-supplemented little owls in areas with a low proportion of food-rich habitat. In contrast, supplemented little

Table 3.1. Model output of the biweekly survival model. n = 125 individuals, 67 females and 58 males. BS = breeding season. Variables whose 95% credible interval excludes zero are highlighted by bold print.

	Posterior mean	CrI	f
Detection submodel			
Intercept 2009	1.160	0.834 – 1.496	-
Intercept 2010-2013	2.313	2.142 – 2.491	-
Males	0.354	0.098 – 0.610	0.997
Recovery probability	0.623	0.523 – 0.719	-
Survival submodel			
Intercept BS	1.593	0.938 – 2.266	-
Intercept REST	2.517	1.854 – 3.206	-
Intercept WINTER	1.889	0.990 – 2.856	-
Males BS	**0.686**	**0.082 – 1.314**	**0.988**
Males REST	0.527	-0.089 – 1.168	0.952
Males WINTER	-0.281	-1.298 – 0.733	0.708
Food supplementation	**0.827**	**0.310 – 1.377**	**0.999**
Food-rich habitat	0.010	-0.252 – 0.280	0.523
Food-rich habitat:food suppl. BS	**0.787**	**0.001 – 1.590**	**0.975**
Food-rich habitat:food suppl. REST	0.038	-0.692 – 0.775	0.540
Food-rich habitat:food suppl. WINTER	**-1.109**	**-2.115 – -0.072**	**0.982**
Field size	0.026	-0.267 – 0.309	0.578
Structural richness	0.156	-0.465 – 0.809	0.680
Clutch size	0.198	-0.050 – 0.446	0.942
Clutch size:food suppl. BS	0.032	-0.718 – 0.820	0.526
Clutch size:food suppl. REST	-0.617	-1.359 – 0.174	0.940
Clutch size:food suppl. WINTER	0.916	-0.319 – 2.180	0.925
Body mass	0.109	-0.100 – 0.322	0.842
Age	**0.865**	**0.389 – 1.325**	**1.000**
Age^2	**-0.109**	**-0.176 – -0.039**	**0.999**
Summer home-range size	0.093	-0.339 – 0.542	0.655
Summer home-range size:males	0.511	-0.127 – 1.156	0.942
Winter home-range size	0.105	-0.335 – 0.549	0.678

owls showed a higher survival with increasing amount of food-rich habitat near the nest (Table 3.1, Fig. 3.2). Second, while the effect of food supplementation in the breeding season and in winter was independent from clutch size, survival rates during the rest of the year were only increased in individuals with small clutches (Table 3.1, Fig. A3.1, Appendix A3). Field size and structural richness did not affect adult survival (Table 3.1).

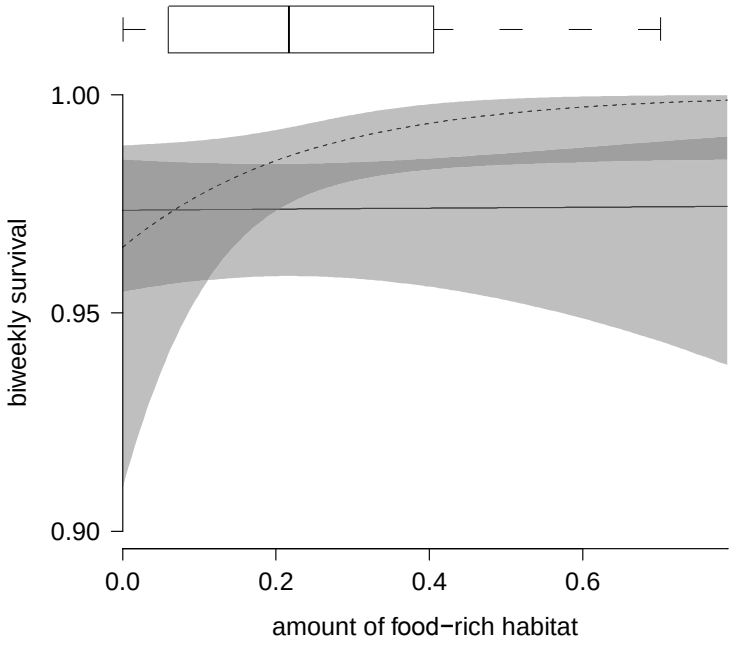

Figure 3.2. Biweekly survival rates of un-supplemented (solid line) and food-supplemented little owls (dashed line) during the breeding season in relation to the amount of food-rich habitat around the nest. Model output for the average between males and females is shown. Grey polygons represent the 95% CrI. The boxplot above the graph shows the distribution of the raw data.

Individual characteristics, clutch size and home-range size

The age of the observed little owls ranged from one eight years. There was a quadratic relationship between age and survival of adult little owls, irrespective of sex (Table 3.1, Fig. 3.3). Thus, little owls at intermediate ages (two to six years) had the highest survival, whereas the survival of first year owls and old owls (seven years or above) was reduced. While a lot of first breeders were observed, the sample size of old little owls was small: 13 little owls survived at least to an age of six years, whereas only one female was recovered dead at the age of seven, and one female at the age of eight.

There was only low support for a relationship between survival and body mass (Table 3.1). Individual survival was slightly positively correlated with clutch size (Table 3.1). In males, survival was positively correlated with summer home-range size (Table 3.1,

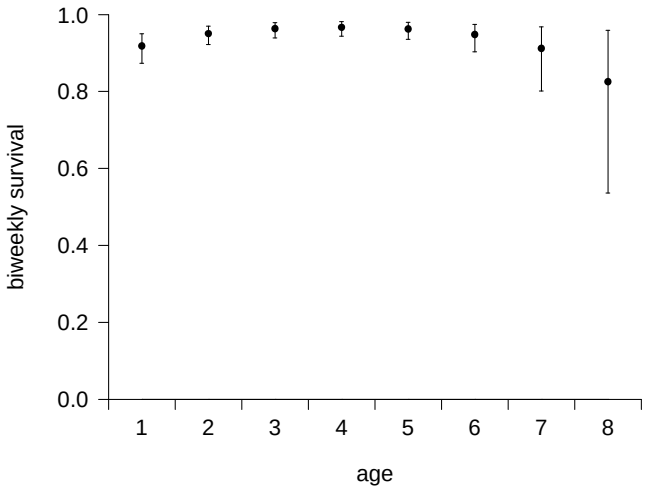

Figure 3.3. Age-dependent biweekly survival rates of females little owls during the breeding season. Error bars indicate the 95% CrI..

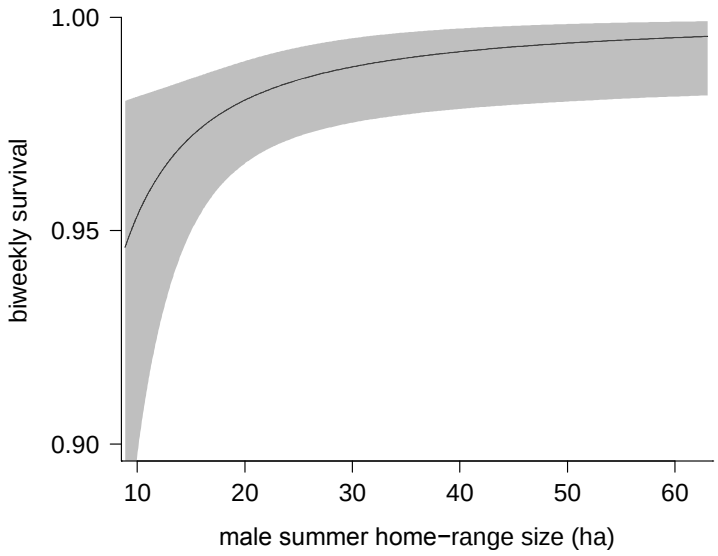

Figure 3.4. Relationship between male home-range size and biweekly survival during the breeding season. Grey polygons represent the 95% CrI.

Fig. 3.4). In contrast, there was no correlation between female survival and summer home-range size or between the survival of either sex and winter home-range size.

Derived yearly survival

By multiplying the biweekly survival rates for the different periods according to the two sexes and the experimental status, we estimated the annual survival of adult little owls. Females without food supplementation had a yearly survival of 0.568 [0.400 – 0.703], males had a yearly survival of 0.702 [0.558 – 0.802]. In contrast, the yearly survival of

food-supplemented females was 0.768 [0.627 – 0.876] and that of males 0.846 [0.745 – 0.921] (Fig. 3.5). Thus, food supplementation increased the survival of females by 15% [-15% – 42%] and the survival of males by 10% [-10% – 31%].

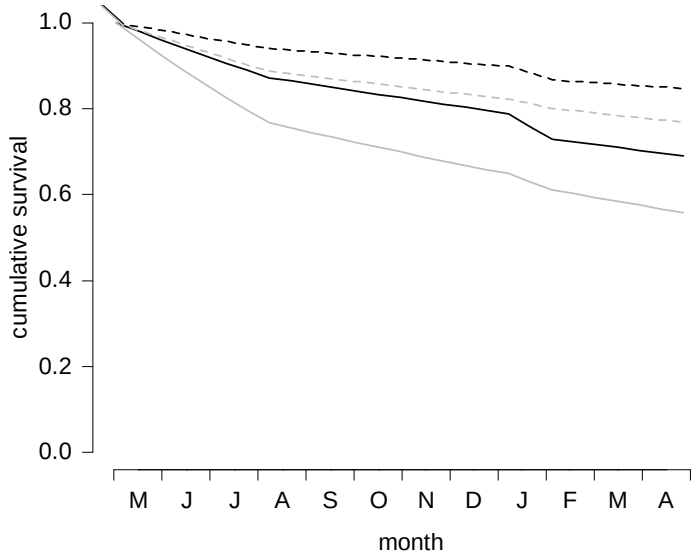

Figure 3.5. Cumulative survival of male (black) and female (grey) adult little owls from May to April of the subsequent year. Solid lines indicate the model output for parents of broods that did not receive food supplementation, whereas dashed lines represent parents of food-supplemented broods.

Discussion

Using experimental food supplementation during the nestling period we demonstrate that the energy supply during the breeding season is not only essential for juvenile survival (Thorup *et al.* 2010; Perrig *et al.* 2014): food supplementation during the nestling phase also increased the survival rate of both female and male adult little owls not only in the breeding season, but also over the whole annual cycle. During the breeding season, only adults in above-average habitats profited from food supplementation. Females showed a lower survival than males, mainly during the breeding season. Yearlings and adults older than six years had reduced survival compared to adults at medium ages. Finally, the estimated yearly survival of food-supplemented and unsupplemented adults revealed that the reduced food-stress during the breeding season increased female survival by 15% and male survival by 10%. To our knowledge, this is the first study demonstrating both an immediate effect of nestling food supplementation on adult survival during the breeding season and a carry-over effect on later stages in the annual cycle.

Yearly survival rates of unsupplemented males estimated from our model were well within the range of the survival rates of little owls estimated in previous studies (0.61 and 0.69 in two Swiss populations, 0.66 and 0.67 in two German populations: Schaub *et al.* 2006; 0.75 in the Netherlands: Le Gouar *et al.* 2010; 0.68 in Denmark: Thorup *et al.* 2013). In contrast to previous studies, we found a sex difference in annual survival: survival rates of female little owls were considerably lower than those of males, mainly due to lower survival probability during the breeding season. This suggests that, in our study area, females incur higher reproductive costs than males. Our survival model confirmed the two periods of reduced survival for adult little owls found in previous studies (Glue 1973; Exo & Hennes 1980; Thorup *et al.* 2013), the breeding season and wintertime. Similar to the analysis of Exo & Hennes (1980), little owl mortality in our study was also increased from mid-January to mid-February. In winter, longer periods of closed snow cover limit the access to small mammals (Korpimäki 1986). Accordingly, winter snow cover affected juvenile survival in our study area (Perrig 2015). Closer analysis of the adult mortalities in winter revealed that little owls often died within or after extended periods of frost, when the temperatures did not exceed 0° Celsius. Such periods are expected to cause increased energetic costs for the maintenance of body temperature. Thus, we suggest that a combination of low resource availability and high energetic demands of thermoregulation causes mortalities mainly near the end of winter.

Experimental brood size reduction and food supplementation often reduce the parental effort (Dawson & Bortolotti 2002; Brommer *et al.* 2004; Eldegard & Sonerud 2010; Santangeli *et al.* 2012). In case of brood size reduction, parents need to feed fewer nestlings compared to control broods, whereas food supplementation increases the nutritional state of the nestlings. Therefore, parents in both cases need to bring less food to the nest. Due to the reduced work load of the parents, the two experimental treatments may affect parental survival (Daan *et al.* 1996; Low *et al.* 2010). There is strong evidence

that the work load of little owl parents is reduced by high natural food supply (Chapters 1 and 2; Staggenborg 2014), and by food supplementation (Chapter 2; Jacobsen *et al.* 2016). Besides reducing the energetic costs, food supplementation may also reduce predation if adults need to cover shorter distances during foraging flights. In contrast to studies investigating the effect of brood size manipulations on parental survival (review in Santos & Nakagawa 2012), we found that both female and male little owls profit from food supplementation during the nestling phase, corroborating the finding that both sexes reduce their parental effort in response to food supplementation (Jacobsen *et al.* 2016). Since food supplementation resulted in elevated survival rates of both parents, we suggest that the behavioural adjustments of little owl parents to food supplementation allowed them to allocate more energy to their somatic condition, thereby increasing survival.

The interaction between food-rich habitat and food supplementation suggests that natural food availability plays a role in shaping the costs of reproduction. This might be interpreted in the light of differential parental investment. If the surrounding habitat is poor, the additional energy supplied to the brood seems to be allocated entirely to the nestlings. With increasing amounts of food-rich habitat, parents start allocating some of the additional energy to self-maintenance, which is supported by the patterns of provisioning and mass decrease in different habitats (Chapter 2, Staggenborg 2014). Consistent with a recent study showing that reproductive success in home-ranges of limited size is reduced (see Chapter 1), we found a positive correlation between male summer home-range size and survival. The interactions found in this study suggest that in situations of restricted food conditions (small home-ranges, low proportion of grasslands) the survival costs for parents are increased. These results point towards exceptionally high parental investment in constraining habitat situations.

The benefits gained by the experiment during the breeding season also affected subsequent periods in the year: food supplementation not only increased parental survival

during the breeding season, but also during winter and during the rest of the year. Recent physiological studies may explain such carry-over effects. Supplemented parents might be able to build up fat reserves (Brommer *et al.* 2004; Eldegard & Sonerud 2010; Santangeli *et al.* 2012), or to allocate more energy to moulting, resulting in feathers of higher quality and thermoregulatory properties (Dawson et al. 2000), linked to improved winter survival (Nilsson & Svensson 1996). Alternatively, food supplementation might reduce the oxidative stress linked to reproductive effort (Alonso-Alvarez *et al.* 2004), the susceptibility to diseases (Descamps *et al.* 2009), or the erosion of telomeres (Reichert et al. 2014). Despite indications for these physiological mechanisms, clear links between physiological costs of reproduction and survival of the parents are still missing.

In contrast to the adults, the effect of nestling food supply did not carry over on juvenile survival during the rest of the year (Perrig 2015). Food supplementation affects juveniles and adults differently. Juveniles profit directly from additional food and are able to invest the additional energy into structural development, body condition, or both. In contrast, parents profit indirectly from food supplementation as a result from the reduced work load, energy, and time they need to invest into food provisioning of the young. However, both direct and indirect effects result in increased energy availability for supplemented individuals. The finding of Perrig et al. (2014) that supplemented nestlings in our study area have significantly longer wings than unsupplemented nestlings lends some support to the hypothesis that juveniles invest some of the additional energy into structural growth. In addition, juvenile survival until the next breeding season may be determined by other factors (e.g. ecological conditions during natal dispersal, predation risk). If selection pressure acts more strongly on structural development than on body condition for juveniles, long-term physiological consequences might not be discernible due to the early mortality of poorly developed individuals.

We have some evidence for a positive relationship between individual quality and adult survival. Such a relationship may be linked to the ability of high quality individuals to acquire more resources or to acquire and defend a better territory (van Noordwijk & de Jong 1986; Hamel *et al.* 2009). In this study, we found a positive trend between adult survival and clutch size. Moreover, male survival probability was positively correlated with summer home-range size. Our experimental approach is expected to reduce the parental effort irrespective of individual quality. Accordingly, the effect of food supplementation on parental survival did not depend on clutch size.

Our results highlight the importance of breeding season food supply for the fate of parent birds and thus, for key parameters of population dynamics. We show that reproduction, i.e. providing the young with food, has survival costs for the adults, and that these survival costs depend on the quality of the habitat. As a consequence, habitat quality in terms of food supply during the breeding season not only affects population productivity by regulating clutch size and juvenile survival, it also affects the demographic structure and the turn-over of the population by regulating adult survival. Thus, at the population level, the distribution and availability of high quality, food-rich habitat patches across the landscape has a strong effect on both productivity and turn-over. We suggest that spatial heterogeneity in habitat quality results in spatial heterogeneity in survival prospects of adult little owls.

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References

Alonso-Alvarez, C., Bertrand, S., Devevey, G., Prost, J., Faivre, B. & Sorci, G. (2004) Increased susceptibility to oxidative stress as a proximate cost of reproduction. *Ecology Letters*, **7,** 363-368.

Bock, A., Naef-Daenzer, B., Keil, H., Korner-Nievergelt, F., Perrig, M. & Grüebler, M.U. (2013) Roost site selection by little owls *Athene noctua* in relation to environmental conditions and life-history stages. *Ibis*, **155,** 847-856.

Brommer, J.E., Karell, P. & Pietiäinen, H. (2004) Supplementary fed Ural owls increase their reproductive output with a one year time lag. *Oecologia*, **139,** 354-358.

Brooks, S.P. & Gelman, A. (1998) General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics*, **7,** 434-455.

Daan, S., Deerenberg, C. & Dijkstra, C. (1996) Increased daily work precipitates natural death in the kestrel. *Journal of Animal Ecology*, **65,** 539-544.

Davis, S.E., Nager, R.G. & Furness, R.W. (2005) Food availability affects adult survival as well as breeding success of parasitic jaegers. *Ecology*, **86,** 1047-1056.

Dawson, A., Hinsley, S.A., Ferns, P.N., Bonser, R.H.C. & Eccleston, L. (2000) Rate of moult affects feather quality: a mechanism linking current reproductive effort to future survival. *Proceedings of the Royal Society of London B: Biological Sciences*, **267,** 2093-2098.

Dawson, R. & Bortolotti, G. (2002) Experimental evidence for food limitation and sex-specific strategies of American kestrels (*Falco sparverius*) provisioning offspring. *Behavioral Ecology and Sociobiology*, **52,** 43-52.

De Steven, D. (1980) Clutch Size, Breeding Success, and Parental Survival in the Tree Swallow (*Iridoprocne bicolor*). *Evolution*, **34,** 278-291.

Descamps, S., Gilchrist, H.G., Bêty, J., Buttler, E.I. & Forbes, M.R. (2009) Costs of reproduction in a long-lived bird: large clutch size is associated with low survival in the presence of a highly virulent disease. *Biology Letters*, **5,** 278-281.

Dhindsa, M.S. & Boag, D.A. (1990) The effect of food supplementation on the reproductive success of black-billed magpies *Pica pica*. *Ibis*, **132,** 595-602.

Doligez, B., Clobert, J., Pettifor, R.A., Rowcliffe, M., Gustafsson, L., Perrins, C.M. & McCleery, R.H. (2002) Costs of reproduction: Assessing responses to brood size manipulation on life-history and behavioural traits using multi-state capture-recapture models. *Journal of Applied Statistics*, **29,** 407-423.

Eldegard, K. & Sonerud, G.A. (2010) Experimental increase in food supply influences the outcome of within-family conflicts in Tengmalm's owl. *Behavioral Ecology and Sociobiology*, **64,** 815-826.

Exo, K.-M. & Hennes, R. (1980) Beitrag zur Populationsökologie des Steinkauzes (*Athene noctua*) - eine Analyse deutscher und niederländischer Ringfunde. *Die Vogelwarte*, **30,** 162-179.

Ghalambor, C.K. & Martin, T.E. (2001) Fecundity-survival trade-offs and parental risk-taking in birds. *Science*, **292,** 494-497.

Glue, D.E. (1973) Seasonal mortality in four small birds of prey. *Ornis Scandinavica*, **4,** 137-146.

Hamel, S., Côté, S.D., Gaillard, J.M. & Festa-Bianchet, M. (2009) Individual variation in reproductive costs of reproduction: high-quality females always do better. *Journal of Animal Ecology*, **78,** 143-151.

Hanssen, S.A., Hasselquist, D., Folstad, I. & Erikstad, K.E. (2005) Cost of reproduction in a long-lived bird: incubation effort reduces immune function and future reproduction. *Proceedings of the Royal Society of London B: Biological Sciences*, **272,** 1039-1046.

Hegner, R.E. & Wingfield, J.C. (1987) Effects of brood-size manipulations on parental investment, breeding success, and reproductive endocrinology of house sparrows. *The Auk*, **104,** 470-480.

Hipkiss, T., Hörnfeldt, B., Eklund, U. & Berlin, S. (2002) Year-dependent sex-biased mortality in supplementary-fed Tengmalm's owl nestlings. *Journal of Animal Ecology*, **71,** 693-699.

Homberger, B., Jenni, L., Duplain, J., Lanz, M. & Schaub, M. (2014) Food unpredictability in early life increases survival of captive grey partridges (*Perdix perdix*) after release into the wild. *Biological Conservation*, **177,** 134-141.

Jacobsen, L.B., Chrenková, M., Sunde, P., Šálek, M. & Thorup, K. (2016) Effects of food provisioning and habitat management on spatial behaviour of Little Owls during the breeding season. *Ornis Fennica*, **93,** 121-129.

Kellner, K. (2015) jagsUI: a wrapper around rjags to streamline JAGS analyses. https://github.com/kenkellner/jagsUI.

Kenward, R.E. (2001) *A manual for wildlife radio tagging*. Academic Press, London, UK.

Kéry, M. & Schaub, M. (2012) *Bayesian population analysis using WinBUGS: A hierarchical perspective*. Academic Press, Oxford, UK.

Kitaysky, A.S., Piatt, J.F., Hatch, S.A., Kitaiskaia, E., Benowitz-Fredericks, Z.M., Schultz, M.T. & Wingfield, J.C. (2010) Food availability and population processes: Severity of nutritional stress during reproduction predicts survival of long-lived seabirds. *Functional Ecology*, **24,** 625-637.

Korpimäki, E. (1986) Gradients in population fluctuations of Tengmalm's owl *Aegolius funereus* in Europe. *Oecologia*, **69,** 195-201.

Le Gouar, P., Schekkerman, H., van der Jeugd, H., Boele, A., van Harxen, R., Fuchs, P., Stroeken, P. & van Noordwijk, A.J. (2010) Long-term trends in survival of a declining population: The case of the little owl (*Athene noctua*) in the Netherlands. *Oecologia*, 1-11.

Lebreton, J.D., Almeras, T. & Pradel, R. (1999) Competing events, mixtures of information and multistratum recapture models. *Bird Study*, **46,** S39-S46.

Low, M., Arlt, D., Eggers, S. & Pärt, T. (2010) Habitat-specific differences in adult survival rates and its links to parental workload and on-nest predation. *Journal of Animal Ecology*, **79,** 214-224.

Martin, T.E. (1987) Food as a limit on breeding birds: A life-history perspective. *Annual Review of Ecology and Systematics*, **18,** 453-487.

Martin, T.E. (1995) Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs*, **65,** 101-127.

Martins, T.L.F. & Wright, J. (1993) Cost of reproduction and allocation of food between parent and young in the swift (Apus apus). *Behavioral Ecology*, **4,** 213-223.

Naef-Daenzer, B., Früh, D., Stalder, M., Wetli, P. & Weise, E. (2005) Miniaturization (0.2 g) and evaluation of attachment techniques of telemetry transmitters. *Journal of Experimental Biology*, **208,** 4063-4068.

Naef-Daenzer, B. & Grüebler, M.U. (2014) Effects of radio-tag characteristics and sample size on estimates of apparent survival. *Animal Biotelemetry*, **2,** 1-9.

Naef-Daenzer, B., Korner-Nievergelt, F., Fiedler, W. & Grüebler, M.U. (2016) Bias in ring-recovery studies: causes of mortality of little owls (Athene noctua) and implications for population assessment. *Journal of Avian Biology*.

Nilsson, J.A. & Svensson, E. (1996) The Cost of Reproduction: A New Link between Current Reproductive Effort and Future Reproductive Success. *Proceedings of the Royal Society of London B: Biological Sciences*, **263,** 711-714.

Oro, D. & Furness, R.W. (2002) Influences of food availability and predation on survival of kittiwakes. *Ecology*, **83,** 2516-2528.

Perrig, M. (2015) *Juvenile survival and onset of natal dispersal in little owls (Athene noctua) in relation to nestling food supply*. PhD thesis, University of Zurich, Zurich, Switzerland.

Perrig, M., Grüebler, M.U., Keil, H. & Naef-Daenzer, B. (2014) Experimental food supplementation affects the physical development, behaviour and survival of little owl *Athene noctua* nestlings. *Ibis*, **156,** 755-767.

Plummer, M. (2003) JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. *Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003)*, March, 20-22.

R Core Team. (2015) R: A language and environment for statistical computing. https://www.R-project.org/.

Reichert, S., Stier, A., Zahn, S., Arrive, M., Bize, P., Massemin, S. & Criscuolo, F. (2014) Increased brood size leads to persistent eroded telomeres. *Frontiers in Ecology and Evolution*, **2**.

Roff, D. (1993) *Evolution of life histories: theory and analysis*. Springer Science & Business Media.

Šálek, M. & Schröpfer, L. (2008) Population decline of the little owl (Athene noctua Scop.) in the Czech Republic. *Polish Journal of Ecology*, **56,** 527-534.

Santangeli, A., Hakkarainen, H., Laaksonen, T. & Korpimäki, E. (2012) Home range size is determined by habitat composition but feeding rate by food availability in male Tengmalm's owls. *Animal Behaviour*, **83,** 1115-1123.

Santos, E.S.A. & Nakagawa, S. (2012) The costs of parental care: A meta-analysis of the trade-off between parental effort and survival in birds. *Journal of Evolutionary Biology*, **25,** 1911-1917.

Schaub, M., Ullrich, B., Knotzsch, G., Albrecht, P. & Meisser, C. (2006) Local population dynamics and the impact of scale and isolation: A study on different little owl populations. *Oikos*, **115**.

Schifferli, L., Grüebler, M.U., Meijer, H.A.J., Visser, G.H. & Naef-Daenzer, B. (2014) Barn Swallow Hirundo rustica parents work harder when foraging conditions are good. *Ibis*, **156,** 777-787.

Schönn, S., Scherzinger, W., Exo, K.-M. & Rottraut, I. (1991) *Der Steinkauz: Athene noctua*. A. Ziemsen Verlag, Wittenberg, Germany.

Sheldon, B.C. & Verhulst, S. (1996) Ecological immunology: costly parasite defences and trade-offs in evolutionary ecology. *Trends in Ecology & Evolution*, **11,** 317-321.

Staggenborg, J. (2014) *Bewegungs- und Raumnutzungsmuster adulter Steinkäuze (Athene noctua) während der Brutzeit in Abhängigkeit des Habitattyps*. MSc thesis, Albert-Ludwigs-Universität Freiburg, Freiburg, Germany.

Stearns, S.C. (1989) Trade-offs in life-history evolution. *Functional Ecology*, **3,** 259-268.

Sundell, J., Huitu, O., Henttonen, H., Kaikusalo, A., Korpimäki, E., Pietiäinen, H., Saurola, P. & Hanski, I. (2004) Large-scale spatial dynamics of vole populations in Finland revealed by the breeding success of vole-eating avian predators. *Journal of Animal Ecology*, **73,** 167-178.

Thorup, K., Pedersen, D., Sunde, P., Jacobsen, L.B. & Rahbek, C. (2013) Seasonal survival rates and causes of mortality of Little Owls in Denmark. *Journal of Ornithology*, **154,** 183-190.

Thorup, K., Sunde, P., Jacobsen, L.B. & Rahbek, C. (2010) Breeding season food limitation drives population decline of the little owl *Athene noctua* in Denmark. *Ibis*, **152**.

Van Nieuwenhuyse, D., Génot, J.-C. & Johnson, D.H. (2008) *The Little Owl: conservation, ecology and behaviour of Athene noctua*. Cambridge University Press, New York, USA.

van Noordwijk, A.J. & de Jong, G. (1986) Acquisition and allocation of resources: Their influence on variation in life history tactics. *The American Naturalist*, **128,** 137-142.

Wiehn, J. & Korpimäki, E. (1997) Food limitation on brood size: Experimental evidence in the Eurasian kestrel. *Ecology*, **78,** 2043-2050.

Zmihorski, M., Romanowski, J. & Osojca, G. (2009) Habitat preferences of a declining population of the little owl, *Athene noctua* in Central Poland. *Folia Zoologica*, **58,** 207-215.

Appendix A3: Additional results

Table A3.1. Output of the full and first reduced model. BS = breeding season: May – August, REST: September – mid-January, mid-February – April, WINTER: mid-January – mid-February, f = proportion of the posterior distribution on the same side of zero as the mean.

	Full model			First reduced model		
	Posterior mean	CrI	f	Posterior mean	CrI	f
Detection submodel						
Intercept 2009	1.158	0.833 – 1.498		1.159	0.837 – 1.496	
Intercept 2010-2013	2.312	2.140 – 2.490		2.313	2.141 – 2.491	
Detection males	0.354	0.099 – 0.609	0.997	0.355	0.100 – 0.612	0.997
Recovery probability	0.623	0.524 – 0.718		0.623	0.523 – 0.718	
Survival submodel						
Intercept BS	1.611	0.880 – 2.358		1.664	0.994 – 2.343	
Intercept REST	2.692	1.944 – 3.461		2.610	1.931 – 3.305	
Intercept WINTER	2.067	1.077 – 3.105		1.978	1.065 – 2.943	
Males BS	0.819	-0.206 – 1.864	0.941	0.657	-0.007 – 1.350	0.974
Males REST	0.749	-0.277 – 1.800	0.922	0.497	-0.181 – 1.191	0.924
Males WINTER	0.072	-1.190 – 1.330	0.546	-0.237	-1.285 – 0.830	0.673
Food supplementation BS	0.558	-0.265 – 1.439	0.903	0.691	0.061 – 1.356	0.985
Food supplementation REST	0.699	-0.195 – 1.655	0.934			
Food supplementation WINTER	0.879	-0.460 – 2.285	0.897			
Food suppl.:males BS	0.871	-0.496 – 2.316	0.890	0.518	-0.439 – 1.519	0.851
Food suppl.:males REST	0.210	-1.099 – 1.577	0.617			
Food suppl.:males WINTER	0.097	-1.462 – 1.685	0.546			
Food-rich habitat BS	-0.059	-0.557 – 0.454	0.594	0.037	-0.311 – 0.395	0.577
Food-rich habitat Rest	0.242	-0.295 – 0.811	0.804			
Food-rich habitat Winter	-0.052	-0.961 – 0.889	0.548			
Food-rich habitat:males BS	-0.132	-0.851 – 0.602	0.642	-0.101	-0.595 – 0.394	0.656
Food-rich habitat:males REST	-0.164	-0.954 – 0.66	0.660			
Food-rich habitat:males Winter	0.169	-0.944 – 1.332	0.610			
Food-rich habitat: food suppl. BS	1.046	0.048 – 2.088	0.980	0.934	0.039 – 1.861	0.980
Food-rich habitat:food suppl. REST	-0.119	-1.050 – 0.827	0.601	0.103	-0.675 – 0.891	0.598
Food-rich habitat:food suppl. WINTER	-0.865	-2.184 – 0.454	0.901	-0.992	-2.048 – 0.100	0.963

Table A3.1 continued

	Full model			First reduced model		
	Posterior mean	CrI	f	Posterior mean	CrI	f
Food-rich habitat:food suppl.:males BS	-0.122	-1.576 – 1.379	0.568			
Food-rich habitat:food suppl.:males REST	0.410	-0.937 – 1.778	0.724			
Food-rich habitat:food suppl.:males WINTER	-0.792	-2.406 – 0.809	0.834			
Field size BS	0.022	-0.598 – 0.623	0.532	0.044	-0.423 – 0.489	0.581
Field size REST	-0.087	-0.777 – 0.576	0.593			
Field size WINTER	0.117	-0.964 – 1.131	0.595			
Field size:males BS	-0.376	-1.311 – 0.538	0.790	0.148	-0.499 – 0.797	0.672
Field size:males REST	0.412	-0.560 – 1.349	0.803			
Field size:males WINTER	0.356	-1.023 – 1.669	0.704			
Field size:food suppl. BS	-0.264	-1.087 – 0.531	0.738	-0.313	-0.935 – 0.298	0.842
Field size:food suppl. REST	-0.189	-1.137 – 0.736	0.652			
Field size:food suppl. WINTER	-0.612	-1.972 – 0.708	0.814			
Field size:food suppl.:males BS	0.835	-0.324 – 1.986	0.923	0.303	-0.586 – 1.158	0.757
Field size:food suppl.: males REST	-0.220	-1.478 – 1.018	0.635	0.164	-0.906 – 1.148	0.633
Field size:food suppl.: males WINTER	-0.530	-2.129 – 1.037	0.743	-0.487	-1.893 – 0.821	0.750
Structural richness BS	0.638	-0.397 – 1.745	0.882	0.150	-0.630 – 0.968	0.639
Structural richness REST	-0.117	-1.149 – 0.946	0.591			
Structural richness WINTER	0.450	-1.094 – 2.062	0.709			
Structural richness:males BS	0.137	-1.274 – 1.582	0.570	-0.047	-1.158 – 1.099	0.536
Structural richness:males REST	-0.119	-1.556 – 1.376	0.569			
Structural richness: males WINTER	-0.185	-1.911 – 1.607	0.588			
Structural richness: food suppl. BS	-0.365	-1.852 – 1.171	0.686	0.271	-0.904 – 1.480	0.671
Structural richness: food suppl. REST	0.389	-1.062 – 1.863	0.698			
Structural richness: food suppl. WINTER	0.535	-1.216 – 2.333	0.721			
Structural richness: food suppl.:males BS	0.389	-1.390 – 2.206	0.662			
Structural richness:food suppl.:males REST	0.687	-1.020 – 2.441	0.782			
Structural richness:food suppl.:males WINTER	0.319	-1.509 – 2.161	0.633			

Table A3.1 continued

	Full model			First reduced model		
	Posterior mean	CrI	f	Posterior mean	CrI	f
Clutch size BS	0.321	-0.138 – 0.786	0.915	0.235	-0.075 – 0.546	0.931
Clutch size REST	0.147	-0.340 – 0.630	0.725			
Clutch size WINTER	0.111	-0.803 – 1.027	0.594			
Clutch size:males BS	-0.462	-1.170 – 0.231	0.904	-0.371	-0.975 – 0.226	0.889
Clutch size:males REST	0.311	-0.400 – 1.024	0.805	0.183	-0.421 – 0.782	0.725
Clutch size:males WINTER	0.293	-0.836 – 1.432	0.693	0.209	-0.658 – 1.104	0.677
Clutch size:food suppl. BS	0.192	-0.675 – 1.107	0.661	0.110	-0.662 – 0.923	0.602
Clutch size:food suppl. REST	-0.660	-1.599 – 0.293	0.914	-0.763	-1.545 – 0.068	0.964
Clutch size: food suppl. WINTER	0.633	-0.856 – 2.159	0.793	0.849	-0.493 – 2.217	0.891
Clutch size:food suppl.: males BS	-0.356	-1.728 – 1.013	0.696			
Clutch size:food suppl.: males REST	-0.228	-1.562 – 1.110	0.631			
Clutch size:food suppl.: males WINTER	0.717	-0.922 – 2.358	0.805			
Body mass	-0.022	-0.307 – 0.262	0.558	0.100	-0.111 – 0.319	0.818
Body mass:males	0.234	-0.214 – 0.703	0.840			
Age	0.890	0.383 – 1.392	1.000	0.826	0.362 – 1.289	1.000
Age^2	-0.109	-0.180 – -0.036	0.998	-0.103	-0.170 – -0.034	0.998
Age:males	-0.141	-0.907 – 0.619	0.642			
Age^2:males	0.016	-0.114 – 0.149	0.589			
Summer home-range size	0.122	-0.322 – 0.583	0.697	0.084	-0.353 – 0.539	0.639
Summer home-range size:males	0.519	-0.165 – 1.201	0.932	0.542	-0.117 – 1.205	0.946
Winter home-range size	0.301	-0.249 – 0.867	0.856	0.122	-0.316 – 0.568	0.703
Winter home-range size:males	-0.439	-1.269 – 0.399	0.849			

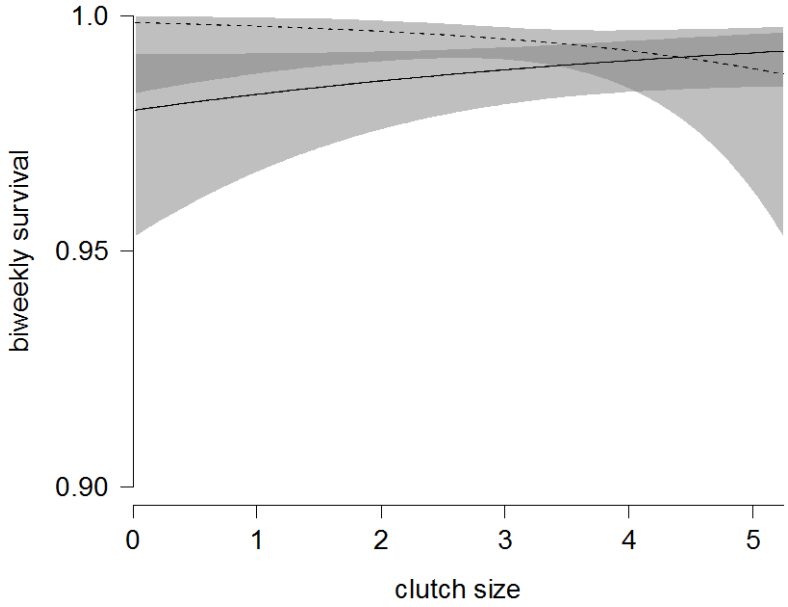

Figure A3.1. Biweekly survival rate of adult little owls during the rest of the year (September–mid-January and mid-February–April) in relation to clutch size. The dashed line represents the survival of parents whose nestlings received food supplementation during the previous breeding season, the solid line the survival of those without food supplementation. Grey polygons indicate the 95% CrI. Due to the high survival of parents of large clutches and the low sample size of food supplemented individuals with large clutches, survival differences were only apparent for small to medium sized clutches.

Supplement 3: BUGS code of the final biweekly survival model

```
model {

   # ------------------------------------------------
   # Parameters:
   # s: true survival probability
   # r: recovery probability
   # p: detection probability
   # ------------------------------------------------
   # States (S):
   # 1 alive in study area
   # 2 recently dead and recovered
   # 3 recently dead, but not recovered, or dead (absorbing)
   # Observations (O):
   # 1 seen alive
   # 2 recovered dead
   # 3 neither seen nor recovered
   # ------------------------------------------------


   # Define state-transition and observation matrices
   for (i in 1:nind){
      # Define probabilities of state S(t+1) given S(t)
      for (t in f[i]:(l[i]-1)){
         ps[1,i,t,1] <- s[i,t]
         ps[1,i,t,2] <- (1-s[i,t])*r[i,t]
         ps[1,i,t,3] <- (1-s[i,t])*(1-r[i,t])

         ps[2,i,t,1] <- 0
         ps[2,i,t,2] <- 0
         ps[2,i,t,3] <- 1

         ps[3,i,t,1] <- 0
         ps[3,i,t,2] <- 0
         ps[3,i,t,3] <- 1

      } # t

      for (t in f[i]:l[i]){
   # Define probabilities of O(t) given S(t)
         po[1,i,t,1] <- p[i,t]
         po[1,i,t,2] <- 0
         po[1,i,t,3] <- 1-p[i,t]
```

```
        po[2,i,t,1] <- 0
        po[2,i,t,2] <- 1
        po[2,i,t,3] <- 0

        po[3,i,t,1] <- 0
        po[3,i,t,2] <- 0
        po[3,i,t,3] <- 1
    } #t
} #i

# Likelihood
for (i in 1:nind){
     for (t in (f[i]+1):l[i]){
       # State process: draw S(t) given S(t-1)
       z[i,t] ~ dcat(ps[z[i,t-1], i, t-1,])
    } #t

    for (t in f[i]:l[i]){
       # Observation process: draw O(t) given S(t)
       y[i,t] ~ dcat(po[z[i,t], i, t,])
    } #t
} #i

# Priors and constraints
for(i in 1:nind){
    for (t in f[i]:(l[i]-1)){
       logit(s[i,t]) <-  a.s[period[t]]  + beta.males.period.s[period[t]] * male[i] +
                         beta.food.sup.s * food.sup[i,index.year[t]] +
                         beta.prop.green.s * prop.green.s[i,t] +
                         beta.prop.green.food.sup.s[period[t]] * prop.green.s[i,t] *
                         food.sup[i,index.year[t]] +
                         beta.field.size.s * field.size.s[i,t] +
                         beta.structural.richness.s * structural.richness[i,t]  +
                         beta.clutch.size.s * clutch.size.s[i,index.year[t]] +
                         beta.clutch.size.food.sup.s[period[t]] * clutch.size.s[i,index.year[t]] *
                         food.sup[i,index.year[t]] +
                         beta.bodymass.s * bodymass.s[i,index.year[t]] +
                         beta.age.s * age[i,index.year[t]] +
                         beta.age.sq.s * age.squared[i,index.year[t]] +
                         beta.summer.hrsize.s * summer[t] *
                         summer.hrsize[i,index.year[t]] +
                         beta.summer.hrsize.males.s * summer[t] *
                         summer.hrsize[i,index.year[t]] * male[i] +
                         beta.winter.hrsize.s * winter[t] * winter.hrsize[i,index.year[t]]
```

```
        r[i,t] <- mean.r
    } #t

for (t in f[i]:l[i]){
    logit(p[i,t]) <- a.p[period2[t]] + beta.males.p * period3[t] * male[i]
    } #t
} #i


# Priors for survival
for(i in 1:3){
    a.s[i] ~ dnorm(0, 1)
    beta.males.period.s[i] ~ dnorm(0, 1)
    beta.prop.green.food.sup.s[i] ~ dnorm(0, 1)
    beta.clutch.size.food.sup.s[i] ~ dnorm(0, 1)
}

beta.food.sup.s ~ dnorm(0, 1)
beta.prop.green.s ~ dnorm(0, 1)
beta.field.size.s ~ dnorm(0, 1)
beta.structural.richness.s ~ dnorm(0, 1)
beta.clutch.size.s ~ dnorm(0, 1)
beta.bodymass.s ~ dnorm(0, 1)
beta.age.s ~ dnorm(0, 1)
beta.age.sq.s ~ dnorm(0, 1)
beta.summer.hrsize.s ~ dnorm(0, 1)
beta.summer.hrsize.males.s ~ dnorm(0, 1)
beta.winter.hrsize.s ~ dnorm(0, 1)

# Priors for recovery
mean.r ~ dunif(0, 1)

# Priors for detection probability
for(i in 1:2){
    a.p[i] ~ dnorm(0, 1)}

beta.males.p ~ dnorm(0, 1)

} #model
```

Chapter 4

Causes and consequences of breeding dispersal in little owls (Athene noctua)

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To be submitted

Keywords: Habitat quality, multi-state mark-recapture model, reproductive success, ringing data, site fidelity, telemetry data

Abstract

Breeding dispersal occurs in a wide variety of species. Nonetheless, its mechanisms are still poorly understood and the direct causes as well as the evolutionary consequences of breeding dispersal are often unclear. Previous studies suggest that reproductive failure may act as a proximate cause of breeding dispersal. Thus, if reproduction depends on habitat quality, dispersal rates may be higher in poor compared to high quality habitats, and dispersing individuals might acquire a higher quality territory. Combining the data of a four year telemetry study in Southern Germany (n = 181 individuals) with long-term data from six ringing projects in Germany and the Netherlands (between 12 and 27 years; n = 977 individuals), we analysed the patterns, causes, and consequences of breeding dispersal in the little owl (*Athene noctua*). We applied a Bayesian multi-state model, which incorporates detection probabilities and combines marked recapture and dead recoveries. Estimated value of the overall breeding dispersal rate was 20% [95% credible interval: 14 – 26%]. Breeding dispersal was increased after brood loss, and individuals that had changed previously were more likely to do so again. In contrast, breeding dispersal rate was not affected by habitat quality, presumably because habitat quality affects the number of offspring rather than causing brood loss. Moreover, dispersing individuals did not acquire a nest site surrounded by higher quality habitat. Mainly as a consequence of the reproductive failure prior to dispersal, dispersing individuals increased their reproductive success compared to the previous year: on average, they reared 0.6 more fledglings after dispersal than before. Depending on habitat-linked brood loss, the rates of breeding dispersal may be considerable. We conclude that while natal dispersal accounts for most of the dynamics between populations, breeding dispersal strongly contributes to the small scale dynamics and turn-over within little owl populations.

Introduction

Although breeding dispersal, the movement of adult individuals between consecutive breeding attempts (Greenwood & Harvey 1982), occurs in a wide variety of species (birds: Greenwood & Harvey 1982; Paradis et al. 1998; Pakanen et al. 2011; Bötsch, Arlettaz & Schaub 2012; Cline et al. 2013; mammals: Gese & Mech 1991; Berteaux & Boutin 2000; insects: McCauley 2010) and may affect population dynamics (Dale *et al.* 2005), it is still poorly understood (Clobert *et al.* 2001; Calabuig *et al.* 2008). Each year, adult individuals have to decide whether to stay in their home-range or to move to a new one. These movement decisions can be affected by ecological conditions of the home-range such as the availability of food or nesting sites (Korpimäki 1993), predation pressure (Weisser 2001), or the presence of a suitable mate (Pärt & Gustafsson 1989) as well as by intrinsic factors such as the age or experience of the adult individual (Calabuig *et al.* 2008).

For a proper understanding of the mechanisms underlying breeding dispersal and its importance for both the individual and the population level, two different aspects of breeding dispersal need to be studied: proximate causes and consequences (Pasinelli *et al.* 2007). Several proximate causes for breeding dispersal have been proposed. Adults might disperse in response to poor reproductive success, caused by low habitat quality, low mate quality, or both (Forero *et al.* 1999; Calabuig *et al.* 2008). Accordingly, dispersal rate would be higher in poor habitats compared to high quality habitats. This leads to the hypothesis that dispersers attempt to acquire a new territory of higher quality or to find a new mate, thereby increasing their reproductive success compared to the preceding reproductive attempt. Alternatively, individuals might disperse in response to intraspecific competition. Assuming that more experienced individuals are better at acquiring or defending a territory, young individuals would be predicted to disperse more frequently (Greenwood & Harvey 1982; Forsman *et al.* 2002). As a result, weak or uncompetitive

individuals might be forced to disperse to lower quality habitats. Besides these proximate causes, there might also be individual consistency in dispersal behaviour (Doligez & Pärt 2008), for example if the dispersal propensity is genetically determined, as assumed by theoretical models of dispersal evolution (e.g. McPeek & Holt 1992). Thus, individuals that have moved before might be more likely to disperse in the future (Doligez & Pärt 2008; Pakanen *et al.* 2011).

In an evolutionary context, breeding dispersal is expected to evolve if dispersers gain a fitness benefit compared to philopatric individuals. At the same time, dispersal might be costly in terms of increased mortality during the dispersal and at a new, unfamiliar site (Daniels & Walters 2000; Yoder *et al.* 2004; Avril *et al.* 2012). The ratio between benefits and costs is expected to depend on the state of the individual as well as the environmental conditions. Potential proximate benefits of breeding dispersal include the acquisition of a higher quality mate, territory, or nest site (Payne & Payne 1993; Blakesley *et al.* 2006). However, there is conflicting evidence for the adaptive value of breeding dispersal: while individuals of some species profit from dispersing (Pärt & Gustafsson 1989; Forero *et al.* 1999; Valcu & Kempenaers 2008; Calabuig *et al.* 2008), other studies found no fitness differences between dispersers and philopatric individuals (Payne & Payne 1993).

In this study, we combined data of a telemetry study within one area in Germany with ringing data from six different areas in Germany and the Netherlands to investigate the patterns, causes, and consequences of breeding dispersal in little owls (*Athene noctua*). Under the general hypothesis that breeding dispersal is an adapted trait of the reproductive behaviour, we made the following predictions for causes and consequences of breeding dispersal. According to the reproduction hypothesis, we predicted that unsuccessful birds disperse more frequently than successful ones, that dispersal rate is higher in low quality habitats than in high quality habitats, and that dispersing little owls have higher reproductive success and / or acquire a territory of higher quality compared to

the previous reproductive attempt. Based on the competition hypothesis, we predicted that first year breeders show a higher dispersal rate than older birds. Finally, based on the hypothesis of individual consistency in dispersal behaviour, we predicted that little owls that have changed their nest site before are more prone to disperse again. Our results give insights into the patterns, causes and consequences of breeding dispersal in little owls.

Methods

Study species and study areas

The little owl occurs in open areas across Europe (Van Nieuwenhuyse *et al.* 2008). Central European little owls traditionally breed in tree cavities or buildings (Van Nieuwenhuyse *et al.* 2008). Where breeding sites are scarce, nest boxes are successfully used as a conservation measure (Gottschalk *et al.* 2011).

Most previous studies on breeding dispersal rely on ringed or colour-banded birds (e.g. Blakesley *et al.* 2006; Eeva *et al.* 2008; Cline *et al.* 2013), potentially underestimating dispersal rates and overestimating mortality if adults leave the study area or breed in unsupervised breeding sites (Pakanen *et al.* 2011). In this study, we combined telemetry data and ring recapture data: A telemetry study within the District of Ludwigsburg (Baden-Württemberg, Southern Germany: 48°53′43″N, 9°11′45″E) provided detailed reencounter data. In addition, ring recapture data from six different little owl ringing projects were available for analysis: Erpolzheim (ER: 49°29′20″N, 8°13′15″E), Köngen / Wendlingen (KW: 48°40′56″N, 9°21′54″E), Lahr (LA: 48°20′20″ N, 7°52′12″E), Rheinhessen (RH: 49°50′38″N, 7°52′23″E), and Wolfschlugen (WS: 48°39′09″N, 9°17′35″E) in Germany, as well as Winterswijk (WW: 51°58′17″N, 6°43′14″E) in the Netherlands. Study durations, exact numbers and sex of individuals as well as the numbers of occupied nest boxes within each area are given in Table A4.1 (see Appendix A4).

Recapture data and definition of breeding dispersal

Telemetry data was summarized as individual annual reencounter histories. In addition, we recorded the reproductive success of each breeding attempt (if available the number of fledglings, otherwise a binary variable for success: 0 in case of failure, 1 if at least one nestling survived). Similarly, the ring recapture data included all recaptures of adults little owls during nest controls, the coordinates of the recapture as well as the reproductive success at the according nest. Mean home-range sizes of adults in our study area were 19.7 ha in summer and 29.7 ha in winter (see Chapter 1). To distinguish nest site changes within a territory from dispersal events, only movements to a nest site farther than 300 m from the previous nest (i.e. nests that are situated outside an area of 28.3 ha around the previous nest) were considered breeding dispersal events. Dispersal distances were calculated with the function spDistsN1 from package sp in R (R Core Team 2015).

Habitat classification

Recent studies on little owls showed that orchards, meadows and vineyards are favourable for little owls whereas arable fields are less profitable (Finck 1990; Apolloni 2013; Staggenborg 2014; Chapter 2). Food abundance is positively correlated with the proportion of orchards and meadows (Apolloni 2013). Therefore, breeding sites were categorized into high quality habitat (more than 50% covered by orchards, meadows or vineyards) and low quality habitats (less than 50% covered by orchards, meadows or vineyards) using imagery of Google Earth (Version 7.1.5.1557, © Google 2015).

Statistical procedures

Multi-state model

Bayesian multi-state models allow simultaneous modelling of detection probability, survival, and site fidelity (i.e. 1 - dispersal rate), thereby accounting for imperfect detection

(Lebreton *et al.* 2009). We developed an individual-based multi-state model based on the theory of Lebreton et al. (1999) and code provided in Kéry & Schaub (2012), which combines marked recapture and dead recoveries. In order to account for the methodological differences, we estimated separate breeding dispersal rates, survival rates, and detection probabilities for the two methods, telemetry and ringing. To simplify the analysis, we considered the first observation of individuals with unknown age as their first breeding attempt. Therefore, detection of the first breeding attempt was set to one. Our model included five different observations based on five true states (Table 4.1). The logit link function was used to model the effect of different covariates on detection probability, survival probability, and site fidelity probability. Instead of setting one region as the intercept and including a factor to estimate the deviation of the other regions from this intercept, we included region-specific intercepts for the detection probability to account for the sampling efforts of each region. In addition to these region-specific intercepts, detection probability was modelled as a function of sex, reproductive success, and an interaction between the two. We estimated site fidelity probability of birds of different ages

Table 4.1. Observations and true states of the multi-state model

	Observation	True state
1	Captured as first breeder	First breeder
2	Recaptured at the same nest site as the previous year	Alive after staying at the same site
3	Recaptured at a different nest site than the previous year	Alive after a breeding dispersal event
4	Recovered dead	Recently dead and recovered
5	Neither recaptured nor recovered	Dead (absorbing state)

(first breeders vs. older birds) and birds followed with different methods (telemetry vs. ring recapture) separately, including an interaction between the two. Therefore, we included age- and method-specific intercepts. Furthermore, site fidelity probability was modelled as a function of sex, success, and habitat whereas the survival probability was modelled as a function of habitat and sex. In addition, we allowed for an interaction between the method and the different factors explaining detection, survival, and site fidelity probability. Only three individuals were recovered dead after or during a dispersal event, all of which were followed by telemetry. Consequently, we were not able to disentangle the survival rates of owls that stayed at the same nest site and dispersing owls.

In a single reduction step, interactions with an f-value (i.e. proportion of simulations on the same side of zero as the mean) below 0.9 were removed. Models were run in JAGS (Plummer 2003), controlled by the package jagsUI (Kellner 2015) in R (R Core Team 2015). As MCMC settings we used 100’000 iterations, a burn-in of 50’000 iterations, a thinning parameter of ten and three chains. Convergence of the Markov chains was checked with Brooks-Rubin-Gelman diagnostics (Brooks & Gelman 1998). For the output of the full model see Table B4.1 (Appendix B4), for the code of the multi-state model see Supplement 4.

Dispersal distances and determinants of reproductive success

Linear mixed models were applied to investigate whether the dispersal distance was related to the sex of the individual, the habitat or the reproductive success before the dispersal event, or the habitat after the dispersal event. Prior to analysis, dispersal distance (in metres) was log-transformed. An individual random effect accounted for multiple dispersal events of the same individual. In addition, we used a generalized linear mixed model with binomial error structure and logit link to test whether reproductive

success was linked to the habitat. Function sim of package arm was used to calculate credible intervals.

Results

In total, 132 individuals (71 females, 61 males) were followed by telemetry and 977 individuals (666 females, 177 males, and 134 individuals of unknown sex) were repeatedly captured throughout the ringing studies (Table 4.2). Out of these 1109 individuals, 425 adult little owls (330 females, 71 males and 24 individuals of unknown sex) were observed in more than one year, yielding a total of 806 potential breeding dispersal events (i.e. observations of the same individual in two consecutive years). While most of these individuals were recaptured between two and four times, one individual was observed over fourteen years. Furthermore, a total of 89 adult little owls were recovered dead.

Table 4.2. Summary of the recapture data of the seven regions. Values represent the total numbers (including individuals of unknown sex), numbers of females and males are given inside the brackets.

Region	Single recapture	Multiple recaptures	Recovered dead	Dispersers	Multiple dispersers
Ringing data					
ER	143 (94/23)	59 (49/4)	3 (2/0)	17 (16/0)	3 (3/0)
KW	44 (11/12)	9 (1/0)	3 (1/0)	5 (1/0)	0
LA	125 (68/32)	90 (68/18)	1 (1/0)	21 (17/4)	4 (4/0)
RH	53 (34/15)	22 (19/2)	1 (1/0)	5 (5/0)	0
WS	49 (26/8)	8 (7/1)	2 (0/1)	1 (1/0)	0
WW	206 (137/50)	169 (152/12)	21 (13/5)	13 (12/1)	3 (3/0)
Telemetry data					
LB	64 (37/27)	68 (34/34)	61 (38/23)	16 (7/9)	1 (0/1)
Total	733 (435/188)	425 (330/71)	89 (55/27)	78 (59/14)	11 (10/1)

Detection and recovery probability

There was some variation in the detection probability of adult little owls depending on the region (Table 4.3). The detection probability of individuals followed by telemetry was markedly higher than the recapture probability of ringed individuals in the ringing studies (Fig. 4.1). Females rearing a successful brood were detected more often than unsuccessful females. There was some support from the model that this relationship did not occur in males (posterior mean [95% credible interval] of the interaction males:reproductive success -0.83 [-1.93 – 0.21], f = 0.94). In addition, there was some support that the reencounter probability of unsuccessful males was higher than that of unsuccessful females (effect of sex: 0.58 [-0.21 – 1.47], f = 0.92). The recovery probability of dead individuals in the ringing projects was low (0.05 [0.03 – 0.07]). In contrast, more than two thirds of the individuals monitored with telemetry were recovered after their death (0.71 [0.61 – 0.80]).

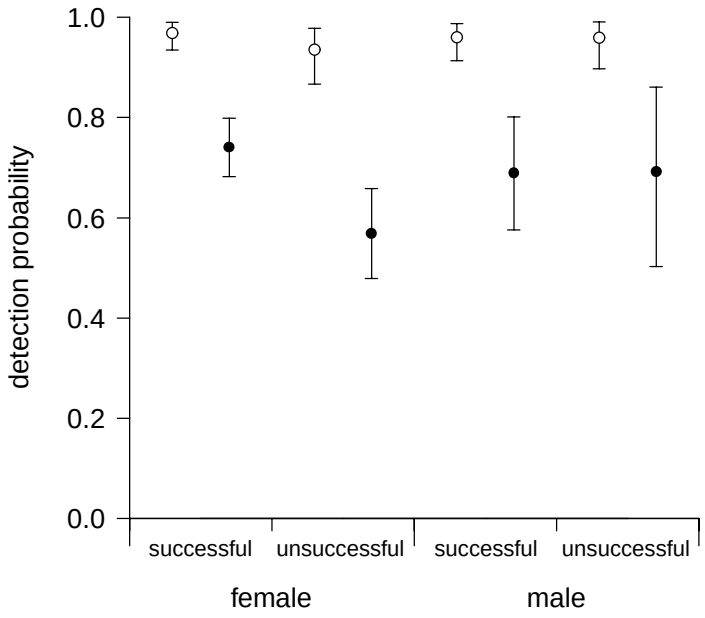

Figure 4.1. Detection probabilities of little owls followed by telemetry (empty circles) and individuals captured during ringing studies (filled circles) in relation to sex and reproductive success. The intercept for the detection of little owls in ringing studies was averaged across all six areas. Error bars represent the 95% credible intervals.

Table 4.3. Posterior means, SDs and 95% credible intervals (CrI) of the multi-state model.

Variable	Mean	SD	CrI
Detection probability			
Region			
Intercept ER	0.113	0.222	-0.311 – 0.560
Intercept KW	0.428	0.456	-0.432 – 1.357
Intercept LA	0.102	0.226	-0.330 – 0.552
Intercept LB (= telemetry)	2.772	0.495	1.873 – 3.804
Intercept RH	0.318	0.406	-0.444 – 1.142
Intercept WS	0.268	0.394	-0.466 – 1.075
Intercept WW	0.445	0.177	0.112 – 0.803
Males	0.572	0.457	-0.268 – 1.535
Reproductive success	0.781	0.221	0.340 – 1.205
Males:reproductive success	-0.817	0.583	-1.999 – 0.313
Survival rate			
Interaction age:method			
Intercept first breeders (ringing)	0.261	0.116	0.037 – 0.493
Intercept first breeders (telemetry)	-0.282	0.252	-0.774 – 0.209
Intercept older birds (ringing)	0.639	0.091	0.463 – 0.816
Intercept older birds (telemetry)	0.095	0.248	-0.390 – 0.586
Grassland habitat	-0.012	0.118	-0.239 – 0.219
Males (ringing)	-0.959	0.146	-1.245 – -0.676
Males (telemetry)	0.567	0.289	0.005 – 1.145
Site fidelity rate			
Interaction age:method			
Intercept first breeders (ringing)	1.199	0.284	0.661 – 1.766
Intercept first breeders (telemetry)	0.610	0.445	-0.241 – 1.502
Intercept older birds (ringing)	1.876	0.272	1.360 – 2.425
Intercept older birds (telemetry)	0.610	0.432	-0.225 – 1.475
Grassland habitat	-0.239	0.244	-0.718 – 0.244
Males	0.154	0.325	-0.469 – 0.818
Reproductive success	1.222	0.264	0.702 – 1.742
Previous change	-1.599	0.374	-2.328 – -0.855
Recovery rate ER	0.028	0.014	0.008 – 0.062
Recovery rate KW	0.086	0.040	0.025 – 0.180
Recovery rate LA	0.010	0.007	0.001 – 0.026
Recovery rate LB (= telemetry)	0.706	0.049	0.605 – 0.798
Recovery rate RH	0.037	0.025	0.005 – 0.100
Recovery rate WS	0.065	0.036	0.014 – 0.153
Recovery rate WW	0.068	0.014	0.044 – 0.098

Survival probability

For the ringing data, the apparent survival rate of yearling individuals was considerably lower than that of older individuals (0.44 [0.39 – 0.49] and 0.53 [0.50 – 0.58], respectively). There was some support for a similar pattern in individuals followed by telemetry (first breeders: 0.50 [0.40 – 0.60]; older individuals: 0.59 [0.49 – 0.69], f = 0.90). Apparent survival rates of females followed by telemetry were lower than those of females in ringing studies, both for first breeders and older birds (both f = 0.98). In contrast, the apparent survival rates of males calculated from telemetry data were higher than the ones calculated from ring recapture data (f = 1 for both age classes; Fig. 4.2). According to the ringing data, females had a higher apparent survival than males (first year females: 0.56 [0.51 – 0.61], first year males: 0.33 [0.27 – 0.40]; older females: 0.65 [0.62 – 0.68], older males: 0.42 [0.35 – 0.49]; Fig. 4.2), whereas the survival of females estimated from the telemetry data was lower than that of males (first year females: 0.43 [0.31 – 0.55], first year males: 0.57 [0.44 – 0.69]; older females: 0.52 [0.41 – 0.64]; older males: 0.66 [0.54 – 0.77]).

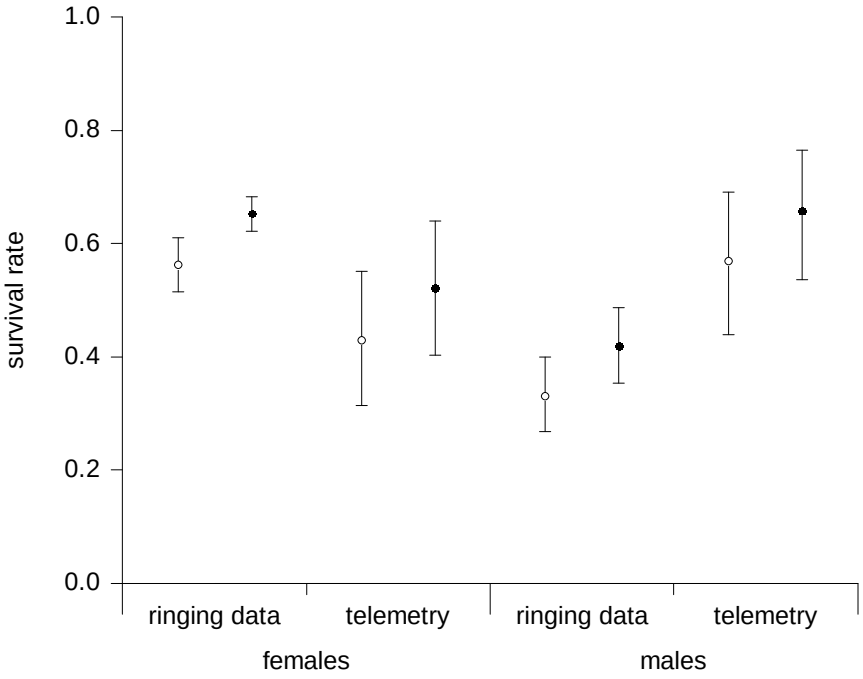

Figure 4.2. Apparent survival of adult little owls in relation to sex and method. Model output was averaged across the different levels of the other covariates. Error bars represent the 95% credible intervals.

Breeding dispersal rate

In total, 78 out of 425 individuals dispersed in 93 out of 806 potential breeding dispersal events. Thus, 18.4 % of the individuals observed over multiple years dispersed at least once after the first reproductive attempt. Numbers of dispersing individuals and dispersal events according to sex and method are summarized in Table 4.4. Apart from the 93 breeding dispersal events, we also observed 49 nest site changes within territories (movement < 300 m).

Table 4.4. Number (percentage) of dispersing individuals and dispersal events according to sex and method of observation.

	Females	Males	Unknown	Total
Individuals				
Ringing data	52 (17.6%)	5 (13.5%)	5 (20.1%)	62 (17.4%)
Telemetry	7 (20.6%)	9 (26.5%)	-	16 (23.5%)
Events				
Ringing data	66 (10.7%)	5 (9.1%)	5 (14.3%)	76 (10.7%)
Telemetry	7 (15.9%)	10 (18.9%)	-	17 (17.5%)

Based on the multi-state model, we neither found a significant difference between the dispersal rate of females and males (f = 0.68), nor between individuals living in habitats of different quality (f = 0.84). Breeding dispersal rate was negatively correlated with the reproductive success in the preceding year, indicating that individuals dispersed upon breeding failure (f = 1.00; Fig. 4.3). Moreover, individuals that had previously dispersed were more likely to disperse again compared to individuals that never changed their breeding territory (f = 1.00; Fig. 4.3, Table 4.3). Since we only had limited data on mates of ringed individuals, we were not able include mate loss as an explanatory variable in the model. Three of the individuals followed by telemetry dispersed after mate loss.

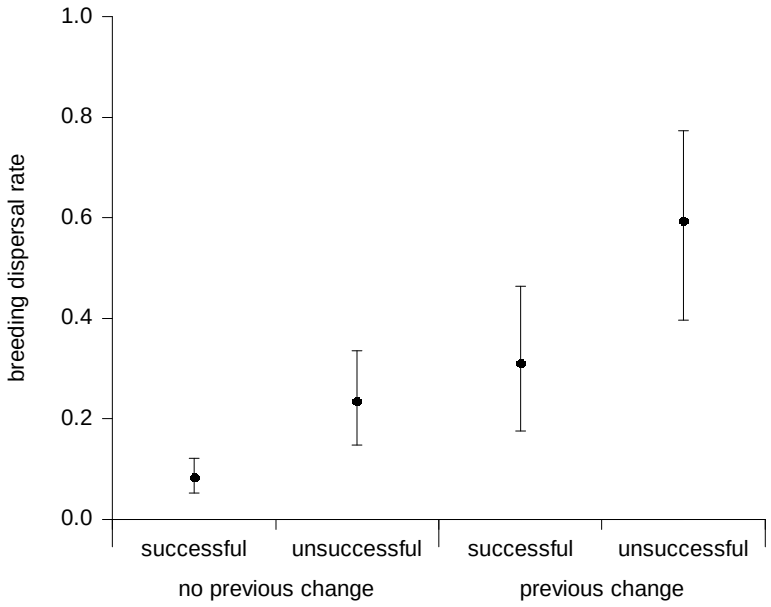

Figure 4.3. Breeding dispersal rate of individuals older than one year in relation to reproductive success and previous change. Model output was averaged across the methods and sexes. Error bars represent the 95% credible intervals.

While ring recovery data indicated that first breeders were more likely to move to a new territory than older birds, this relationship was not found for the telemetry data (difference between the back transformed intercept of the site fidelity rate of first breeders and older birds, ringing data: -0.10 [-0.19 – -0.01], f = 0.99; telemetry data 0.00 [-0.22 – 0.22], f = 0.50; Table 4.3). Finally, the dispersal rates estimated from the telemetry data were higher than those estimated from ringing data, irrespective of age (difference between methods in first breeders: f = 0.90, in older birds: f = 1.00).

Averaged across the seven study sites, roughly 58% of the observed individuals per year were first breeders, whereas 42% were older birds (range of the proportion of first breeders: 30 – 69%). Mean success rate was 0.776, and 1.9% of the individuals showed multiple dispersal events. These data allowed the calculation of an overall annual dispersal rate, irrespective of age, success, and previous dispersal. Overall dispersal rate from one year to the next was 20% [14 – 26%].

Eleven individuals (14% of the dispersing individuals) made multiple movements to a nest box farther than 300 m. Among these multiple dispersal events, ten out of eleven individuals (91%) moved back to a previously occupied territory (i.e. either the same nest

box, or a nest box within 300 m from the previous nest box) at least once: eight individuals (72%) moved away from a nest site and returned later, one individual (9%) changed its nest site four times, including one return to a previous location, and one individual (9%) moved back and forth between two nest sites three times. In five of these cases, little owls moved from high-quality to low-quality habitats and back. Only one individual (9%) moved twice without returning to a previous territory.

Dispersal distance

Dispersal distance did not differ significantly between females, males, and individuals of unknown sex (mean distance ± 1 SD = 1.44 ± 2.22 km, 1.38 ± 1.42 km and 1.30 ± 0.66 km, respectively; Table 4.5), although all four individuals moving further than 5 km were females (maximum = 12.2 km). There was a significant effect of age indicating that dispersal distance decreased with age (Table 4.5). We found no relationship between habitat or success before dispersal and dispersal distance. Moreover, the dispersal distance did not differ between little owls followed by telemetry and those recaptured in the ringing studies. The dispersal distance of multiple dispersers was 0.59 ± 0.45 km, and the distance always decreased in subsequent dispersal events to different nestboxes.

Table 4.5. Linear mixed-effects model investigating the determinants of the breeding dispersal distance. Effects whose 95% CrI excludes zero are indicated by bold print.

	Estimate	SE	CrI
Intercept	7.480	0.267	6.944 – 8.009
Males	0.411	0.390	-0.358 – 1.197
Unknown sex	-0.088	0.560	-1.23 – 1.044
Habitat	-0.133	0.152	-0.443 – 0.161
Success	-0.226	0.199	-0.634 – 0.158
Telemetry	-0.460	0.338	-1.119 – 0.227
Age	**-0.095**	**0.044**	**-0.181 – -0.006**

Random effects:

Individual: n = 69, explained variance = 0.740

Total: n = 83, residual variance = 0.135

Consequences of breeding dispersal

While the reproductive output did not differ significantly between philopatric individuals and dispersers (mean ± SD number of offspring: philopatric parents: 2.4 ± 1.7 fledglings, dispersers: 2.5 ± 1.6 fledglings), a comparison of the change in reproductive output in comparison to the pre-dispersal success revealed a difference between dispersing and philopatric individuals. Only 37% of the philopatric individuals reared more fledglings in the second year, whereas almost half of the dispersing individuals (46%) reared more fledglings after the dispersal than before. On average, dispersers reared 0.61 fledglings more than in the preceding reproductive cycle (CI = 0.05–1.17), whereas the number of fledglings of philopatric little owls did not change significantly (mean = -0.15, CI = -0.33 – 0.03; t-test comparing philopatric individuals and dispersers: $t_{67} = -2.55$, $p = 0.01$).

Dispersing little owls did not acquire a higher quality habitat. While 19% (18 out of 93 individuals) moved from a nest site surrounded by arable fields to a nest site surrounded by orchards, 25% (n = 23) moved from an area dominated by orchards to a nest site surrounded by arable fields. All the other individuals moved within the same habitat quality class (orchard to orchard: 30%, n = 28; arable fields to arable fields: 26%, n = 24).

Discussion

Breeding dispersal of little owls was mainly linked to three different factors. First, as predicted by the reproduction hypothesis, reproductive failure strongly increased the propensity of individuals to disperse. Second, individuals that had already shown breeding dispersal were more likely than others to change their territory again, in agreement with the individual consistency hypothesis. Third, the breeding dispersal rate was linked to the age of the individuals, as predicted by the competition hypothesis: first breeders showed a higher dispersal rate than older individuals. However, this relationship was only apparent in the analysis of recapture data, but not in the analysis of telemetry data. On average the

reproductive success of dispersers was similar to philopatric individuals. However, dispersers reared 0.6 fledglings more after dispersal compared to the preceding year, as predicted by the reproduction hypothesis. Finally, dispersers did not acquire a territory of higher quality: similar proportions of dispersers moved from a high-quality to a low-quality territory as the other way round.

Previous evidence on breeding dispersal in little owls is scarce (Van Nieuwenhuyse *et al.* 2008) and based entirely on ringing data. Dispersal rates found in our study were considerably higher than those found by Kämpfer & Lederer (1988), who reported breeding dispersal for 10.2% of the females and 1.8% of the males. In contrast, six out of 23 adult little owls recaptured by Exo & Hennes (1980) had moved farther than 9 km, corresponding to a dispersal rate of 26%. The highest rates of breeding dispersal were found by Zens (2005) in Northrhine-Westphalia: 19.2% of 73 males and 35.4% of 65 females showed breeding dispersal. Due to the large sample size, the use of telemetry and due to taking detection probability into account, the dispersal rates in our study are expected to be more accurate and less vulnerable to stochastic effects. Breeding dispersal distances in our study corresponded to those found in previous studies (Juillard 1984; Kämpfer & Lederer 1988; Zens 2005). There is only anecdotal evidence for large scale breeding dispersal (e.g. two individuals moving farther then 50 km: Exo & Hennes 1980).

Many species show breeding dispersal in response to reproductive failure (Newton & Marquiss 1982; Forero *et al.* 1999; Blakesley *et al.* 2006; Calabuig *et al.* 2008; Schaub & von Hirschheydt 2009). Such reproductive failure may be caused by direct nest predation or if one of the parents dies, which strongly affects nestling survival (See Chapter 1). Mate loss has been suggested as a potential proximate cause of breeding dispersal (e.g. Forero *et al.* 1999). In this study, we did not have sufficient information about the mates to test for the effect of mate loss on breeding dispersal rate. However, there was some anecdotal data: three individuals followed by telemetry dispersed after mate loss. If predation risk of

the brood or the mate at the current nest site is higher than at alternative sites within normal dispersal distances, dispersal should be favoured after a predation event. In contrast to predation risk, habitat quality in terms of food supply affects the number of offspring, rather than resulting in complete reproductive failure (Chapter 1). Accordingly, individuals in poor habitats did not show an increased dispersal rate, and dispersers did not acquire a higher quality territory after dispersal compared to before.

Our multi-state model indicated that little owls that had previously dispersed were more likely to disperse again compared to philopatric individuals. There are several possible explanations for this pattern. First, there might be individual consistency in dispersal behaviour (Doligez & Pärt 2008). Second, the effect may be due to collinearity in habitat characteristics over a series of reproductive attempts. Within a larger area, individuals may be unable to settle in optimal habitat and consequently be more prone to disperse than individuals in areas with high availability of optimal breeding sites. For example, where predation on juveniles is strong, it is expected to be advantageous to change the nest site frequently, even within the territory. In such areas, the availability of unoccupied nest sites and the conspecific density may limit the opportunities for individuals to disperse.

Dispersing little owls did not achieve a higher reproductive output than philopatric individuals. Nonetheless, due to the low reproductive output before dispersal, dispersing parents increased their individual reproductive success from the year before dispersal to the year after dispersal. Similar patterns were shown for sparrowhawks (*Accipiter nisus*: Newton 2001) and lesser kestrels (*Falco naumanni*: Calabuig *et al.* 2008). We suggest that individuals follow the decision rule “win–stay, lose–switch” (Nowak 1993; Switzer 1993; Chalfoun & Martin 2010), which is mainly beneficial in a highly predictable environment. Our results suggest that breeding dispersal of little owls serves the purpose of augmenting the chances for future reproductive success after reproductive failure.

To closer investigate differences in data sets collected by the two methods, we compared the patterns of detection, survival and breeding dispersal estimated with these two methods. There was large variation in the detection probability of ringed males. Many ringing projects try to keep the disturbance of adult individuals at a minimum. Since females stay in the nest longer, they are often caught while controlling the nest boxes or ringing the juveniles, leading to markedly larger sample sizes for females than for males (see Table 4.2). Unless males are often recaptured after remaining undetected for several years, it is not possible to distinguish between low survival probability and low detection probability. Accordingly, we suggest that the lower apparent survival of males compared to females in the analysis of the ring recapture data in this study is based on the low detection of elusive male owls. The model estimated a higher dispersal rate from the telemetry data compared to the ring recapture data. A possible explanation for this might be the high detection probability of individuals followed by telemetry, which suggests that most, if not all, dispersing individuals were observed. In contrast, breeding dispersal of ringed birds might not always be observed, particularly if dispersing individuals have a higher mortality risk. However, since we did not have access to the ringing data from the site of our telemetry study, we cannot exclude area-specific differences.

Our data confirm the strong site fidelity of adult little owls, with 98% of the little owls staying within 2 km of their previous nest site. However, considering age-structure, success rate and proportion of multiple breeders, little owls showed a dispersal rate of 20% from one to the next year. Depending on habitat-linked brood loss, the rates of breeding dispersal may be considerable, resulting in a high turn-over on a small spatial scale. We conclude that while natal dispersal accounts for most of the dynamics between populations, breeding dispersal strongly contributes to the small scale dynamics and turn-over within little owl populations.

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References

Apolloni, N. (2013) *Landscape use, foraging habitat selection and relationships to food resources in breeding little owls: recognizing the importance of scale for species conservation management*. Thesis, Universität Bern, Bern, Switzerland.

Avril, A., Letty, J., Pradel, R., Léonard, Y., Santin-Janin, H. & Pontier, D. (2012) A multi-event model to study stage-dependent dispersal in radio-collared hares: when hunting promotes costly transience. *Ecology*, **93,** 1305-1316.

Berteaux, D. & Boutin, S. (2000) Breeding dispersal in female North American red squirrels. *Ecology*, **81,** 1311-1326.

Blakesley, J.A., Anderson, D.R. & Noon, B.R. (2006) Breeding dispersal in the California spotted owl. *The Condor*, **108,** 71-81.

Bötsch, Y., Arlettaz, R. & Schaub, M. (2012) Breeding dispersal of Eurasian hoopoes (*Upupa epops*) within and between years in relation to reproductive success, sex, and age. *The Auk*, **129,** 283-295.

Brooks, S.P. & Gelman, A. (1998) General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics*, **7,** 434-455.

Calabuig, G., Ortego, J., Cordero, P.J. & Aparicio, J.M. (2008) Causes, consequences and mechanisms of breeding dispersal in the colonial lesser kestrel, *Falco naumanni*. *Animal Behaviour*, **76,** 1989-1996.

Chalfoun, A.D. & Martin, T.E. (2010) Facultative nest patch shifts in response to nest predation risk in the Brewer's sparrow: a "win-stay, lose-switch" strategy? *Oecologia*, **163,** 885-892.

Cline, M.H., Strong, A.M., Sillett, T.S., Rodenhouse, N.L. & Holmes, R.T. (2013) Correlates and Consequences of Breeding Dispersal in a Migratory Songbird. *The Auk*, **130,** 742-752.

Clobert, J., Danchin, E., Dhondt, A.A. & Nichols, J.D. (2001) *Dispersal*. Oxford University Press, Oxford, UK.

Dale, S., Lunde, A. & Steifetten, Ø. (2005) Longer breeding dispersal than natal dispersal in the ortolan bunting. *Behavioral Ecology*, **16,** 20-24.

Daniels, S.J. & Walters, J.R. (2000) Between-year breeding dispersal in red-cockaded woodpeckers: Multiple causes and estimated cost. *Ecology*, **81,** 2473-2484.

Doligez, B. & Pärt, T. (2008) Estimating fitness consequences of dispersal: a road to 'know-where'? Non-random dispersal and the underestimation of dispersers' fitness. *Journal of Animal Ecology*, **77,** 1199-1211.

Eeva, T., Ahola, M., Laaksonen, T. & Lehikoinen, E. (2008) The effects of sex, age and breeding success on breeding dispersal of pied flycatchers along a pollution gradient. *Oecologia*, **157,** 231-238.

Exo, K.-M. & Hennes, R. (1980) Beitrag zur Populationsökologie des Steinkauzes (*Athene noctua*) - eine Analyse deutscher und niederländischer Ringfunde. *Die Vogelwarte*, **30,** 162-179.

Finck, P. (1990) Seasonal variation of territory size with the little owl (*Athene noctua*). *Oecologia*, **83,** 68-75.

Forero, M.G., Donázar, J.A., Blas, J. & Hiraldo, F. (1999) Causes and consequences of territory change and breeding dispersal distance in the black kite. *Ecology*, **80,** 1298-1310.

Forsman, E.D., Anthony, R.G., Reid, J.A., Loschl, P.J., Sovern, S.G., Taylor, M., Biswell, B.L., Ellingson, A., Meslow, E.C., Miller, G.S., Swindle, K.A., Thrailkill, J.A., Wagner, F.F. & Seaman, D.E. (2002) Natal and breeding dispersal of Northern spotted owls. *Wildlife Monographs*, 1-35.

Gese, E.M. & Mech, L.D. (1991) Dispersal of wolves (*Canis lupus*) in northeastern Minnesota, 1969-1989. *Canadian Journal of Zoology*, **69,** 2946-2955.

Gottschalk, T.K., Ekschmitt, K. & Wolters, V. (2011) Efficient placement of nest boxes for the little owl (*Athene noctua*). *Journal of Raptor Research*, **45,** 1-14.

Greenwood, P.J. & Harvey, P.H. (1982) The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics*, **13,** 1-21.

Juillard, M. (1984) *La chouette chevêche*. Nos Oiseaux, Prangins, Switzerland.

Kämpfer, A. & Lederer, W. (1988) Dismigration des Steinkauzes (*Athene noctua*) in Mittelwestfalen. *Die Vogelwelt*, **109,** 155-164.

Kellner, K. (2015) jagsUI: a wrapper around rjags to streamline JAGS analyses. https://github.com/kenkellner/jagsUI.

Kéry, M. & Schaub, M. (2012) *Bayesian population analysis using WinBUGS: A hierarchical perspective*. Academic Press, Oxford, UK.

Korpimäki, E. (1993) Does nest-hole quality, poor breeding success or food depletion drive the breeding dispersal of Tengmalm's owls? *Journal of Animal Ecology*, **62,** 606-613.

Lebreton, J.D., Almeras, T. & Pradel, R. (1999) Competing events, mixtures of information and multistratum recapture models. *Bird Study*, **46,** S39-S46.

Lebreton, J.-D., Nichols, J.D., Barker, R.J., Pradel, R. & Spendelow, J.A. (2009) Modeling individual animal histories with multistate capture-recapture models. *Advances in Ecological Research*, **41,** 87-173.

McCauley, S.J. (2010) Body size and social dominance influence breeding dispersal in male *Pachydiplax longipennis* (Odonata). *Ecological Entomology*, **35,** 377-385.

McPeek, M.A. & Holt, R.D. (1992) The evolution of dispersal in spatially and temporally varying environments. *The American Naturalist*, **140,** 1010-1027.

Newton, I. (2001) Causes and consequences of breeding dispersal in the sparrowhawk *Accipiter nisus*. *Ardea*, **9,** 143-154.

Newton, I. & Marquiss, M. (1982) Fidelity to Breeding Area and Mate in Sparrowhawks *Accipiter nisus*. *Journal of Animal Ecology*, **51,** 327-341.

Nowak, M. (1993) A strategy of win-stay, lose-shift that outperforms tit-for-tat in the Prisoner's Dilemma game. *Nature*, **364,** 56-58.

Pakanen, V.M., Hildén, O., Rönkä, A., Belda, E.J., Luukkonen, A., Kvist, L. & Koivula, K. (2011) Breeding dispersal strategies following reproductive failure explain low apparent survival of immigrant Temminck's stints. *Oikos*, **120,** 615-622.

Paradis, E., Baillie, S.R., Sutherland, W.J. & Gregory, R.D. (1998) Patterns of natal and breeding dispersal in birds. *Journal of Animal Ecology*, **67**.

Pärt, T. & Gustafsson, L. (1989) Breeding dispersal in the collared flycatcher (*Ficedula albicollis*): Possible causes and reproductive consequences. *Journal of Animal Ecology*, **58**.

Pasinelli, G., Müller, M., Schaub, M. & Jenni, L. (2007) Possible causes and consequences of philopatry and breeding dispersal in red-backed shrikes *Lanius collurio*. *Behavioral Ecology and Sociobiology*, **61,** 1061-1074.

Payne, R.B. & Payne, L.L. (1993) Breeding dispersal in indigo buntings: Circumstances and consequences for breeding success and population structure. *The Condor*, **95**.

Plummer, M. (2003) JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. *Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003)*, March, 20-22.

R Core Team. (2015) R: A language and environment for statistical computing. https://www.R-project.org/.

Schaub, M. & von Hirschheydt, J. (2009) Effect of current reproduction on apparent survival, breeding dispersal, and future reproduction in barn swallows assessed by multistate capture-recapture models. *Journal of Animal Ecology*, **78,** 625-635.

Staggenborg, J. (2014) *Bewegungs- und Raumnutzungsmuster adulter Steinkäuze (Athene noctua) während der Brutzeit in Abhängigkeit des Habitattyps*. MSc thesis, Albert-Ludwigs-Universität Freiburg, Freiburg, Germany.

Switzer, P.V. (1993) Site fidelity in predictable and unpredictable habitats. *Evolutionary Ecology*, **7,** 533-555.

Valcu, M. & Kempenaers, B. (2008) Causes and consequences of breeding dispersal and divorce in a blue tit, *Cyanistes caeruleus*, population. *Animal Behaviour*, **75,** 1949-1963.

Van Nieuwenhuyse, D., Génot, J.-C. & Johnson, D.H. (2008) *The Little Owl: conservation, ecology and behaviour of Athene noctua*. Cambridge University Press, New York, USA.

Weisser, W.W. (2001) The effects of predation on dispersal. *Dispersal* (eds J. Clobert, E. Danchin, A. A. Dhondt & J. D. Nichols), pp. 180-188. Oxford University Press, Oxford, UK.

Yoder, J.M., Marschall, E.A. & Swanson, D.A. (2004) The cost of dispersal: Predation as a function of movement and site familiarity in ruffed grouse. *Behavioral Ecology*, **15,** 469-476.

Zens, K.-W. (2005) *Langzeitstudie (1987-1997) zur Biologie, Ökologie und Dynamik einer Steinkauzpopulation (Athene noctua SCOP. 1769) im Lebensraum der Mechernicher Voreifel*. PhD thesis, Rheinische Friedrich-Wilhelms-Universität, Bonn.

Appendix A4: Additional methods

Table A4.1. Sample sizes, durations, and method of the different studies in Germany as well as the one in the Netherlands (Winterswijk).

Region	Females	Males	Unknown	Nestboxes	Years	Method
Erpolzheim	143	27	32	95	2002-2013	Ringing
Köngen	12	12	29	37	2003-2013	Ringing
Lahr	136	50	29	102	1989-2013	Ringing
Ludwigsburg	99	82	0	126	2009-2013	Telemetry
Rheinhessen	53	17	5	26	1999-2013	Ringing
Wolfschlugen	33	9	15	32	1997-2013	Ringing
Winterswijk	289	62	24	138	1987-2013	Ringing
Total	765	259	134	556		

Appendix B4: Additional results

Table B4.1. Output of the linear mixed model investigating the determinants of the breeding dispersal distance.

Variable	Estimate	SD	CrI
Detection probability			
Region			
Intercept ER	0.181	0.230	-0.258 – 0.648
Intercept KW	0.518	0.456	-0.340 – 1.451
Intercept LA	0.190	0.231	-0.251 – 0.653
Intercept LB (= telemetry)	2.346	0.636	1.141 – 3.651
Intercept RH	0.399	0.408	-0.366 – 1.221
Intercept WS	0.355	0.395	-0.395 – 1.165
Intercept WW	0.516	0.183	0.169 – 0.885
Males (ringing)	0.539	0.466	-0.325 – 1.512
Males (telemetry)	0.369	0.753	-1.070 – 1.878
Reproductive success (ringing)	0.670	0.227	0.221 – 1.108
Reproductive success (telemetry)	1.591	0.749	0.144 – 3.086
Males:reproductive success (ringing)	-0.812	0.580	-1.974 – 0.312
Males:reproductive success (telemetry)	0.285	0.911	-1.473 – 2.087
Survival rate			
Interaction age:method			
Intercept first breeders (ringing)	0.287	0.121	0.054 – 0.528
Intercept first breeders (telemetry)	-0.362	0.273	-0.896 – 0.169
Intercept older birds (ringing)	0.658	0.096	0.469 – 0.848
Intercept older birds (telemetry)	0.015	0.263	-0.504 – 0.532
Grassland habitat (ringing)	-0.053	0.127	-0.300 – 0.194
Grassland habitat (telemetry)	0.234	0.300	-0.342 – 0.83
Males (ringing)	-0.958	0.148	-1.249 – -0.667
Males (telemetry)	0.549	0.288	-0.008 – 1.119
Site-fidelity rate			
Interaction age:method			
Intercept first breeders (ringing)	1.301	0.317	0.690 – 1.924
Intercept first breeders (telemetry)	0.584	0.542	-0.483 – 1.623
Intercept older birds (ringing)	1.949	0.302	1.360 – 2.544
Intercept older birds (telemetry)	0.471	0.557	-0.604 – 1.568
Grassland habitat (ringing)	-0.187	0.274	-0.716 – 0.354
Grassland habitat (telemetry)	-0.374	0.507	-1.381 – 0.624
Males (ringing)	0.161	0.608	-0.978 – 1.406
Males (telemetry)	-0.012	0.571	-1.114 – 1.122

Table B4.1 continued

Variable	Estimate	SD	CrI
Reproductive success (ringing)	1.023	0.312	0.407 – 1.653
Reproductive success (telemetry)	1.387	0.559	0.293 – 2.504
Males:reproductive success (ringing)	-0.023	0.827	-1.572 – 1.673
Males:reproductive success (telemetry)	0.422	0.665	-0.874 – 1.726
Previous change (ringing)	-1.732	0.563	-2.831 – -0.605
Previous change (telemetry)	-0.392	0.875	-2.109 – 1.334
Previous change:repr. success (ringing)	0.283	0.658	-1.039 – 1.559
Previous change:repr. success (telemetry)	-0.367	0.899	-2.113 – 1.397
Recovery rate ER	0.028	0.014	0.008 – 0.060
Recovery rate KW	0.085	0.040	0.024 – 0.178
Recovery rate LA	0.010	0.007	0.001 – 0.027
Recovery rate LB (= telemetry)	0.703	0.049	0.603 – 0.795
Recovery rate RH	0.037	0.026	0.004 – 0.101
Recovery rate WS	0.064	0.035	0.014 – 0.148
Recovery rate WW	0.068	0.014	0.043 – 0.098

ER = Erpolzheim, KW = Köngen / Wendlingen, LA = Lahr, LB = Ludwigsburg,

RH = Rheinhessen, WS = Wolfschlugen and WW = Winterswijk.

Supplement 4: Code of the final multi-state model

```
model {
    # ---------------------------------------------------------
    # Parameters:
    #
    # phi.first: apparent survival of first breeders
    # phi: apparent survival of little owls ≥ 2 years
    #
    # psi.first: site fidelity rate of first breeders
    # psi: site fidelity rate of little owls ≥ 2 years
    #
    # p: recapture probability
    #
    # rec: recovery rate
    # ---------------------------------------------------------
    # States (S):
    # 1 alive at first site
    # 2 alive at same site
    # 3 alive at different site
    # 4 recently dead
    # 5 dead
    #
    # Observations (O):
    # 1 seen as first time breeder
    # 2 seen at same site
    # 3 seen at different site
    # 4 recovered dead
    # 5 not seen
    # ---------------------------------------------------------

    # State space model likelihood
    for (i in 1:nind){
    # State process: draw S(t) given S(t-1)
        for (t in (first[i]+1): last[i]){
            z[i,t] ~ dcat(ps[z[i,t-1], i, t-1,])
        } #t

    # Observation process: draw O(t) given S(t)
        for (t in first[i]: last[i]){
            y[i,t] ~ dcat(po[z[i,t], i, t,])
        } #t
```

```
} #i
# Define state-transition and observation matrices
for (i in 1:nind){
# Define probabilities of state S(t+1) given S(t)
    for (t in first[i]:( last[i]-1)){
        ps[1,i,t,1]  <- 0# [true state, individual, time, state at time t+1]
        ps[1,i,t,2]  <- phi.first[i,t] * psi.first[i,t]
        ps[1,i,t,3]  <- phi.first[i,t] * (1 - psi.first[i,t])
        ps[1,i,t,4]  <- rec[region[i]] * (1 - phi.first[i,t])
        ps[1,i,t,5]  <- (1 - rec[region[i]]) * (1 - phi.first[i,t])

        ps[2,i,t,1]  <- 0
        ps[2,i,t,2]  <- phi[i,t] * psi[i,t]
        ps[2,i,t,3]  <- phi[i,t] * (1 - psi[i,t])
        ps[2,i,t,4]  <- rec[region[i]] * (1 - phi[i,t])
        ps[2,i,t,5]  <- (1-rec[region[i]]) * (1 - phi[i,t])

        ps[3,i,t,1]  <- 0
        ps[3,i,t,2]  <- phi[i,t] * psi[i,t]
        ps[3,i,t,3]  <- phi[i,t] * (1-psi[i,t])
        ps[3,i,t,4]  <- rec[region[i]] * (1 - phi[i,t])
        ps[3,i,t,5]  <- (1-rec[region[i]]) * (1 - phi[i,t])

        ps[4,i,t,1]  <- 0
        ps[4,i,t,2]  <- 0
        ps[4,i,t,3]  <- 0
        ps[4,i,t,4]  <- 0
        ps[4,i,t,5]  <- 1

        ps[5,i,t,1]  <- 0
        ps[5,i,t,2]  <- 0
        ps[5,i,t,3]  <- 0
        ps[5,i,t,4]  <- 0
        ps[5,i,t,5]  <- 1
    } #t

# Define probabilities of O(t) given S(t)
    for (t in first[i]: last[i]){
        po[1,i,t,1]  <- p.first   # [true state, individual, time, observed state]
        po[1,i,t,2]  <- 0
        po[1,i,t,3]  <- 0
        po[1,i,t,4]  <- 0
        po[1,i,t,5]  <- 1-p.first
```

```
            po[2,i,t,1]  <- 0
            po[2,i,t,2]  <- p[i,t]
            po[2,i,t,3]  <- 0
            po[2,i,t,4]  <- 0
            po[2,i,t,5]  <- 1-p[i,t]

            po[3,i,t,1]  <- 0
            po[3,i,t,2]  <- 0
            po[3,i,t,3]  <- p[i,t]
            po[3,i,t,4]  <- 0
            po[3,i,t,5]  <- 1-p[i,t]

            po[4,i,t,1]  <- 0
            po[4,i,t,2]  <- 0
            po[4,i,t,3]  <- 0
            po[4,i,t,4]  <- 1
            po[4,i,t,5]  <- 0

            po[5,i,t,1]  <- 0
            po[5,i,t,2]  <- 0
            po[5,i,t,3]  <- 0
            po[5,i,t,4]  <- 0
            po[5,i,t,5]  <- 1
        } #t
    } #i


    # Priors and constraints
    for(i in 1:nind){
        for (t in first[i]:( last[i]-1)){
            logit(phi.first[i,t])  <- a.phi.first[telemetry[i]] +
                                      beta.habitat.phi * habitat[i,t] +
                                      beta.males.phi[telemetry[i]] * male[i]
            logit(phi[i,t])  <-  a.phi[telemetry[i]] +
                                 beta.habitat.phi * habitat[i,t] +
                                 beta.males.phi[telemetry[i]] * male[i]


    # linear predictors for site fidelity rates
            logit(psi.first[i,t])  <- a.psi.first[telemetry[i]] +
                                      beta.habitat.psi * habitat[i,t] +
                                      beta.males.psi * male[i] +
                                      beta.success.psi * success[i,t]
```

```
        logit(psi[i,t])  <-  a.psi[telemetry[i]] +
                             beta.habitat.psi * habitat[i,t] +
                             beta.males.psi * male[i] +
                             beta.success.psi * success[i,t] +
                             beta.previous.change.psi *
                             (1 - equals(sum(z[i,first[i]:t]), z[i,first[i]]+2*t-2*first[i]))
    } #t


# linear predictors for detection probabilities
    for (t in first[i]: last[i]){
        logit(p[i,t])  <-  a.p[region[i]] +
                           beta.males.p * male[i] +
                           beta.success.p * success[i,t] +
                           beta.success.males.p * success[i,t] * male[i]
    } #t
} #i

# Priors for region-specific intercepts of the detection probability and recovery rate
for(r in 1:nregions){
    rec[r] ~ dnorm(0,1)
    a.p[r] ~ dnorm(0,1)
} #r

# Priors for the method-specific intercepts and predictors
for(m in 1:2){
    a.phi.first[m] ~ dnorm(0,1)
    a.phi[m] ~ dnorm(0,1)
    beta.males.phi[m] ~ dnorm(0,1)

    a.psi.first[m] ~ dnorm(0,1)
    a.psi[m] ~ dnorm(0,1)
} #m

# Priors for the predictors of survival
    beta.habitat.phi ~ dnorm(0,1)

# Priors for the predictors of site fidelity
    beta.males.psi ~ dnorm(0,1)
    beta.success.psi ~ dnorm(0,1)
    beta.habitat.psi ~ dnorm(0,1)
    beta.previous.change.psi ~ dnorm(0,1)
```

```
    # Set detection for the first breeding attempt to 1, since the age birds with unknown
age
    # was considered to be 1 and we did not estimate states before the first observation
        p.first <- 1

    # Priors for the predictors of detection probability
        beta.males.p ~ dnorm(0,1)
        beta.success.p ~ dnorm(0,1)
        beta.success.males.p ~ dnorm(0,1)



    # impute missing values for sex
    for(f in 1:nnosex){
        male[indexnosex[f]] ~ dbern(0.5)
    } #f

    # impute missing values for habitat according to the ratio of habitats in the observed
data
    for(i in 1:nind){
        for(h in 1:nnohabitat[i]){
            habitat[i,indexnohabitat[i,h]] ~ dbern(0.5)
        } #h
    } #i

    # impute missing values for success according to the ratio of success in the observed
data
    for(i in 1:nind){
        for(s in 1:nnosuccess[i]){
            success[i,indexnosuccess[i,s]] ~ dbern(0.776)
        } #s
    } #i
}
```

Chapter 5

Intraguild predator drives forest edge avoidance of a mesopredator

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Key-words: *Athene noctua*; edge effect; food availability; Southern Germany; intraguild predation; little owl; risk effects; *Strix aluco*; tawny owl.

Abstract

Interactions between top predators and mesopredators of the same guild often result in habitat segregation restricting interactions to shared habitat edges. Although negative edge effects are recognized as important spatial patterns in the ecology of fragmented landscapes, the underlying mechanisms of predator-prey interactions resulting in negative edge effects remain unknown. To disentangle top-down effects of intraguild predators and bottom-up effects of shared resources on mesopredator spatial distribution, we recorded the occurrence of tawny owls *Strix aluco* in forests and their prey, the little owl *Athene noctua* in adjacent open areas over two years across 687 km^2 in Southern Germany. We developed a new, asymmetrical dynamic two-species occupancy model investigating spatial interactions while accounting for imperfect detection. Little owl occupancy was strongly reduced within 150 m of forests, but only in the presence of tawny owls. Analysis of over 30,000 telemetry locations of 275 little owls showed that little owls strongly avoided areas closer than 150 m from the forest during range use. These results suggest that the negative edge effect is due to forest edge avoidance rather than direct predation. Potential confounding mechanisms such as food depletion or habitat avoidance at forest edges can be ruled out. Thus, top-down effects caused by avoidance of intraguild top predators shape the spatial distribution of mesopredators such as the little owl. While habitat complexity mitigates multitrophic interactions within habitats, it is expected to reinforce multitrophic interactions between habitats, potentially leading to the suppression of mesopredators from suitable habitats.

Introduction

The spatial structure of species communities is affected by food webs whose predator-prey interactions may act by direct lethal predation or by non-lethal risk effects based on anti-predator behaviour (Creel & Christianson 2008; Cresswell *et al.* 2010). Non-lethal effects include changes in the spatial behaviour of prey such as avoidance of areas of high predation risk (Lima & Dill 1990; Heithaus & Dill 2006; Cresswell *et al.* 2010). Since predation risk varies according to landscape topology, habitat composition, and the abundance of specific predators, prey species constantly adapt their behaviour to a "landscape of fear" (Brown *et al.* 1999; Laundré *et al.* 2001). Perceived predation risk can shape the spatial behaviour of prey at different levels: home-range selection (Fontaine & Martin 2006), habitat use (Willems & Hill 2009), dispersal movements (Otsuki & Yano 2014) and thus, distribution and dynamics of prey animals throughout their lives (Cresswell 2008).

Intraguild predator-prey interactions, i.e. interactions between a top predator and a mesopredator sharing the same food resources (Polis et al. 1989) are intensified by mutual competition for food. In the absence of avoidance behaviour, encounter rates of mesopredators and their intraguild predator at shared foraging sites of high food availability are expected to exceed those of predator and prey with completely distinct diets, resulting in elevated predation risk in intraguild systems (Morris 2005). Compared to simple predator-prey interactions, intraguild predators additionally profit from exclusion of their intraguild prey from shared food patches by reduced depletion (Polis & Holt 1992). Life-history theory predicts that in prey strategies to minimize predation should evolve, for example exploitation of alternative food sources or use of distinct habitats (Korpimäki 1987), depending on the densities of both predator and prey (Heithaus 2001). As a result of increased encounter rates and predation pressure, this should particularly apply to

intraguild systems. However, hitherto investigations of the consequences of predator-prey interactions on range use were rarely based on intraguild systems.

Negative effects of interspecific competition and predation may be reduced by temporal segregation (Fedriani et al. 2000), by small scale behavioural avoidance (Swanson et al. 2014), or by complete habitat segregation (Schoener 1974; Thiollay 1993), all of which reduce the encounter rates between the two species. Structured habitats can further reduce encounter rates and create refuges for prey, thereby mitigating the effect of intraguild predators on prey populations (Janssen *et al.* 2007; Thompson & Gese 2007). Interactions between habitat segregated intraguild predators and their prey are limited to shared habitat edges. Nonetheless, in fragmented landscapes the amount of edge habitat is considerable and interactions at habitat edges may be important determinants of mesopredator spatial behaviour. Although intraguild predation is recognized as an important factor shaping range use of mesopredators (Ritchie & Johnson 2009; Swanson *et al.* 2014), spatial patterns of mesopredators at shared habitat edges remain unknown. Furthermore, it remains unclear if reduced occupancy or prey density near habitat edges is due to direct predation, due to edge avoidance in response to perceived predation risk, or both (Suhonen *et al.* 1994; Lima 2009; Fonderflick *et al.* 2013). Behavioural studies are needed to differentiate between the two mechanisms (Lima & Valone 1991).

Our study aims to close this gap by investigating the interaction between the little owl *Athene noctua* living in open habitat and its intraguild predator, the tawny owl *Strix aluco* inhabiting adjacent forests (Redpath 1995; Van Nieuwenhuyse *et al.* 2008). While tawny owls often forage at the forest edge, little owls avoid forests (e.g. Lack 1946; Zabala *et al.* 2006). We examine three alternative hypotheses explaining this observed forest avoidance: (1) the “avoidance hypothesis” suggests active avoidance of forest edges in response to perceived predation threat (Fontaine & Martin 2006); (2) the “predation hypothesis” assumes predation close to the forest resulting in apparent forest avoidance

(Suhonen et al. 1994); and (3) the “resource hypothesis” attributes the avoidance to the lack of important resources such as food or suitable hunting grounds near the edge (Ries & Sisk 2004). The “resource hypothesis” predicts that both occupancy and individual range use of little owls correspond to the distribution of resources. Thus, inconsistency between range use or occupancy patterns and resource distribution would provide evidence against it. While both the “avoidance hypothesis” and the “predation hypothesis” predict that little owls occupy territories further away from forests inhabited by tawny owls than from forests without tawny owls, only the “avoidance hypothesis” predicts behavioural avoidance during night-to-night range use. In contrast, under the “predation hypothesis” little owls should use their range according to resource availability, whereby individuals foraging close to the forest are predated. Accordingly, increased predation rates at sites close to forests are predicted. To test these predictions, we first developed a novel, asymmetrical dynamic two-species occupancy model based on presence-absence data (an extension of the models of Waddle et al. 2010 and MacKenzie et al. 2003). Second, we analysed data of individual spatial behaviour and survival of little owls from a four-year telemetry study. Third, we investigated the availability of the main little owl food and of the preferred foraging habitats in relation to the distance to the forest edge. Our results give insights into predator avoidance strategies at shared habitat edges and their consequences for range use and distribution of intraguild prey.

Materials and Methods

Study species and study area

The little owl is a small nocturnal owl species of open habitats (Van Nieuwenhuyse et al. 2008). It is a mesopredator feeding on small rodents (mainly *Microtus* spp.), insects, earthworms, and birds (Juillard 1984). Particularly in open areas, where tawny owls frequently prey upon *Microtus* spp. (Petty 1999), the diets of little owls and tawny owls

overlap considerably. Due to its small size, the little owl is susceptible to predation from several larger species, and there is a lot of evidence for little owl predation by tawny owls (Mikkola 1976; Schönn *et al.* 1991). Besides the eagle owl (*Bubo bubo*), which is rare in our study area, the tawny owl is considered as the second most important predator of the little owl (Van Nieuwenhuyse et al. 2008).

Our study was carried out in Southern Germany (District of Ludwigsburg, Baden-Württemberg, 48°53′43″N, 9°11′45″E). The study area with a surface of 687 km^2 is composed of a mosaic of forests (25%), human settlements (17%) and farmland (58%). The agricultural landscape is dominated by fields of intensive agriculture, interspersed with pastures, meadows, orchards, and vineyards (Bock et al. 2013). The little owl subpopulation within our study area currently consists of roughly 220 breeding pairs (H. Keil, *unpublished data*), mostly breeding in artificial nest boxes, which include a protection against martens. While the little owls breeding in nest boxes are being closely monitored, an unknown number of pairs breeds in natural nests within tree cavities every year.

Field methods

Playback procedure

A survey of little owls and tawny owls was conducted in February-March 2012 and 2013 using call playbacks. An overview and details about the selection of the 156 playback sites are given in Fig. A5.1 (see Appendix A5). Each playback site was visited three times using one of three different call sequences of each species (see Appendix A5 for detailed methods). Since the weather conditions can affect the detection probability, the occurrence of precipitation, wind, cloudiness, and the amount of background noise were recorded (variables are defined in Table A5.1, Appendix A5). This approach resulted in a dataset consisting of encounter histories of both species over three visits per year.

Radio tracking

To investigate the range use and direct avian predation of little owls in relation to the distance to the forest edge, point location data of little owls collected in a telemetry study from summer 2009 until summer 2013 were analysed (Bock et al. 2013). Little owls were equipped with very high frequency (VHF) transmitters of own construction (Naef-Daenzer et al. 2005) weighing 6.9 - 7.2 g (corresponding to 4-5% of a bird's body mass), with an operational range of up to 40 km in the field and an expected life span of 400 days. For details about tagging procedures, see Bock et al. (2013). During 2-4 visits per week, each bird was located twice at an interval of 5 minutes by homing in using a 3-element Yagi antenna and a handheld receiver (Kenward 2001). Only night-time locations were considered, amounting to a total of 30,721 locations of 275 little owls (65 females, 58 males, and 152 juveniles).

Remains of depredated individuals were usually found shortly after death, allowing us to distinguish between mammalian and avian predation (Bock et al. 2013). In many cases it was impossible to ascertain, which avian predator was responsible for the predation. Data of 167 little owls with known fate from one year to the next were available for the investigation of mortality rates due to avian predation. Since several birds were followed over multiple years, these data originate from 120 individual adults (63 females, 57 males).

Food abundance

The range use of little owls is expected to vary according to the abundance of food resources. Although little owls have a broad prey spectrum, small mammals generally comprise the largest part of their biomass intake (e.g. Šálek et al. 2010). Therefore, we quantified the number of field signs (i.e. runways and holes) of common voles (*Microtus* spp.) along transects with a width of 0.5 m and a length of 5 m as a proxy for food

abundance (Giraudoux *et al.* 1995; Apolloni 2013). This proxy correlates well with live-trappings (Lambin et al. 2000).

Spatial variables

The distance of each playback site to the closest forest patch (area ≥ 2,500 m^2) was measured in Google Earth (Version 7.1.2.2041, © Google 2013) with an accuracy of 10 m. Points within the forest were assigned negative values corresponding to the distance to the forest edge. Since Central European little owls are often associated with orchards (Gottschalk et al. 2011) and their breeding success correlates with distance to human habitations (Tomé et al. 2004), distances of each playback site to the closest orchard (≥ 6 fruit trees), and to the closest village (≥ 6 houses) were extracted.

To compare the habitat compositions at different distances from the forest and to test whether little owls preferentially use areas at larger distances from the forest, the study area was split into areas of similar distance from the forest. Distance buffers (0-50 m, 50-100 m, …, 450-500 m, > 500 m) were created around forest areas extracted from a land use raster of Baden-Württemberg (adapted from Gottschalk et al. 2011) using ArcGIS 10.0 (ESRI, Redlands, CA, USA). Within each distance buffer, the relative proportion of three habitat types important for little owls (arable fields, orchards, and meadows) was calculated. Since range use of breeding little owls depends on the distance to the nest or roost site (Sunde et al. 2014), the availability of areas at different forest distances and their use were assessed separately for ten distance classes from the little owl nest (see Appendix A5, Fig. A5.2 for details).

Statistical analyses

Occupancy model

We developed a dynamic two-species occupancy model to analyse the presence-absence data of both owl species. Three visits at each playback site allowed quantification of the detection probability. Our model (developed with the help of M. Kéry) accounts for the asymmetrical relationship between predator and prey, extending the parameterization developed by Waddle et al. (2010) to a multi-season model (MacKenzie et al. 2003), thereby creating an asymmetrical dynamic two-species occupancy model. We used colonization (γ; i.e. the rate at which previously unoccupied sites were occupied in the following year) and persistence (φ; i.e. the rate of sites occupied in both years) to model the differences in occupancy (ψ) between year t and year t + 1:

$$\psi_{t+1} = \psi_t * \varphi + (1 - \psi_t) * \gamma \qquad \text{(Eq. 1)}$$

Initial occupancy of tawny owls was given by

$$\mathrm{logit}(\psi_1^{\text{tawny}}) = \alpha_\psi^{\text{tawny}} + \beta_\psi^{\text{tawny}} * \mathrm{cov}_i \quad \text{(Eq. 2)}$$

where cov_i are the different site-specific spatial distance variables described above (i.e. distance to forest, orchard and village). To avoid numerical overflow (Kéry & Schaub 2012), distance variables were standardized (see Appendix A5). Detection probability (p) of tawny owls as well as φ and γ were modelled in an analogous way. Weather and noise variables entered the detection probability model as visit-specific covariates (cov_{ij} in Eqs. 2 and 3). In addition, the little owl detection model included tawny owl occupancy:

$$\mathrm{logit}\left(p^{\text{little}}\right) = \psi_t^{\text{tawny}} * \alpha_{p,+} + \left(1 - \psi_t^{\text{tawny}}\right) * \alpha_{p,-} + \beta_p * \mathrm{cov}_{ij} \qquad \text{(Eq. 3)}$$

The initial occupancy by little owls was modelled as a function of tawny owl presence, site-specific habitat covariates and an interaction between the two:

$$\mathrm{logit}\left(\psi_1^{\text{little}}\right) = \psi_1^{\text{tawny}} * \alpha_{\psi,+} + \left(1 - \psi_1^{\text{tawny}}\right) * \alpha_{\psi,-} + \psi_1^{\text{tawny}} * \beta_{i,\psi,+} * \mathrm{cov}_i + \left(1 - \psi_1^{\text{tawny}}\right) * \beta_{i,\psi,-} * \mathrm{cov}_i \quad \text{(Eq. 4)}$$

Finally, little owl dynamics were modelled depending on tawny owl occupancy:

$$\psi_{t+1}^{\text{little}} = \psi_t^{\text{little}} * \psi_t^{\text{tawny}} * \varphi_+^{\text{little}} + \psi_t^{\text{little}} * \left(1 - \psi_t^{\text{tawny}}\right) * \varphi_-^{\text{little}} + \left(1 - \psi_t^{\text{little}}\right) * \psi_t^{\text{tawny}} * \gamma_+^{\text{little}} + \quad \text{(Eq. 5)}$$

$$\left(1 - \psi_t^{\text{little}}\right) * \left(1 - \psi_t^{\text{tawny}}\right) * \gamma_-^{\text{little}}$$

The symbols + or – represent the presence or absence of tawny owls, respectively.

All models were written in the BUGS language and run in the software JAGS (Plummer 2003) controlled by the package R2jags (Su & Yajima 2012) in R Version 3.0.2. (R Core Team 2012). To reach convergence, the models were run for 1,000,000 iterations with a burn in of 100,000, a thinning parameter of 10, and 3 chains. As priors for intercepts and parameters, we used a uniform distribution from -10 to 10, for the dynamic parameters of the little owls a uniform distribution from 0 to 1. Covariates were sequentially removed from the model if the 95% credible interval of the posterior distribution included 0. Goodness of fit of the final model was assessed using predictive model checking (for the predictive model check see Appendix B5, the data and code to run the final model are given as a supplement).

Range use

Small scale behaviour of little owls near forest edges might provide insight into the mechanism of edge avoidance. Within each distance class from the nest (see Appendix A5, Fig. A5.2), Manly's resource selection ratio W_i, the ratio of used and available habitat was calculated using the package adehabitatHS in R (Manly *et al.* 2002; Calenge 2006). This analysis relates the proportion of locations within each distance buffer from the forest (proportion used) to the proportion of area belonging to the according distance buffer (proportion available).

Avian predation and vole density

Reduced occupancy or range use near forest edges might be caused by direct predation of little owls or low food abundance. Therefore, we investigated if little owls nesting close to the forest were at a higher risk of being killed by avian predators. In four cases, tawny owls were calling repeatedly near the site of recovery of the remains or transmitter, strongly suggesting predation by tawny owls. Since this low sample size did not allow complex modelling, we compared the distance of the nests of these little owls to the rest using a two-sided t-test. Including the data of little owls killed by an unknown avian predator, a generalized linear mixed model (GLMM) with binomial error structure and logit link function was used to relate the occurrence of avian predation to the distance to the forest. Forest distance was log-transformed to improve convergence. Since many individuals were observed over several years, the individual identity was included as a random factor. The distance to the forest edge, sex, and the estimated occurrence of tawny owls nearby (extracted from the occupancy model) were included as fixed factors. To test whether a potential edge effect was due to reduced food abundance in the vicinity of the forest, we added a binary factor (distance < 150 m = 1, n = 159; > 150 m from the forest = 0, n = 3656) to a well-established model investigating which factors affect the frequency of vole signs (Apolloni 2013). This binomial GLMM includes the habitat type (arable field, grassland, orchard and buffer zone) as a fixed factor and the sampling surface as a random factor. Both GLMMs were fit in R using function glmer in package lme4 (Bates et al. 2014).

Results

Detection probability

Precipitation and cloudiness did not affect the detection probability of either owl species. Thus, these factors were removed from the final model. The presence of wind reduced the

Table 5.1. Model estimates and 95% credible intervals (CrI) of the dynamic two-species occupancy model.

Parameter	Predictor†	Posterior mean	Posterior SD	CrI
Tawny owl sub-model				
Detection 2012 (*p*)	intercept	0.73	0.16	0.42 – 1.05
	wind	-1.22	0.44	-2.10 – -0.37
	noise	-0.09	0.36	-0.78 – 0.63
Detection 2013 (*p*)	intercept	0.53	0.18	0.18 – 0.89
	wind	0.58	0.76	-0.82 – 2.19
	noise	-0.98	0.31	-1.59 – -0.37
Occupancy (*ψ*)	intercept	0.42	0.22	-0.01 – 0.87
	forest	-0.39	0.07	-0.54 – -0.26
Persistence (*φ*)	intercept	1.36	0.91	0.28 – 3.79
	city	0.48	0.25	0.13 – 1.11
	forest	-0.62	0.32	-1.47 – -0.24
Colonization (*γ*)	intercept	-0.77	0.47	-1.69 – 0.12
	forest	-0.42	0.18	-0.80 – -0.13
Little owl sub-model				
Detection 2012 (*p*)	intercept +	0.59	0.23	0.15 – 1.04
	intercept –	0.91	0.28	0.38 – 1.47
	noise	-1.06	0.35	-1.73 – -0.38
Detection 2013 (*p*)	intercept +	0.41	0.27	-0.11 – 0.94
	intercept –	0.74	0.26	0.24 – 1.27
	noise	-0.82	0.36	-1.53 – -0.11
Occupancy (*ψ*)	intercept +	1.83	0.59	0.84 – 3.07
	forest +	0.30	0.17	0.06 – 0.59
	forest^2 +	-0.15	0.05	-0.26 – -0.06
	intercept –	0.44	0.37	-0.26 – 1.20
	forest –	-0.05	0.08	-0.21 – 0.10
Persistence (*φ*)	+	0.71	0.08	0.54 – 0.87
	–	0.84	0.08	0.68 – 0.98
	difference	-0.13	0.11	-0.35 – 0.09
Colonization (*γ*)	+	0.10	0.05	0.02 – 0.21
	–	0.18	0.09	0.03 – 0.38
	difference	-0.08	0.10	-0.30 – 0.11

† Predictors in presence and absence of tawny owls are indicated with + and –, respectively.

detection probability of tawny owls in 2012, but not in 2013 (Table 5.1, Appendix C5, Fig. C5.1). Detection of little owls was not affected by wind. High background noise reduced tawny owl detection in 2013 and little owl detection in both years (Table 5.1, Appendix C5, Fig. C5.1). In 81% of the MCMC-simulations, little owl detection was lower in the presence than in the absence of tawny owls (Table 5.1, Appendix C5, Fig. C5.1).

Occupancy pattern

Both the occupancy probability and the year-to-year persistence of tawny owls declined with increasing distance of a playback site to the closest forest patch (Table 5.1). Tawny owl persistence increased with distance from the closest village, whereas their occupancy and colonization rates were not affected (Table 5.1). The colonization rate of previously unoccupied sites by tawny owls was higher inside the forest or near its edge than at greater distances (Table 5.1). In summary, these results confirm the close association of tawny owls with forest habitats.

Little owl occupancy was neither related to the distance to the closest orchard nor to the distance to the closest village. Thus, both covariates were removed from the final model. There was a positive correlation between the presence of little owls and the distance to the forest. However, this relationship only occurred in the presence of tawny owls (Fig. 5.1, Table 5.1). Persistence and colonization rate of little owls were higher in the absence of tawny owls in 88% and 78% of the MCMC-simulations, respectively (Table 5.1).

Potential underlying mechanisms

Range use: behavioural avoidance

Areas close to the nest were strongly preferred: 33.3% of all locations (n = 12,408) were situated within 50 m of an individual's nest. Due to the high abundance of locations in this

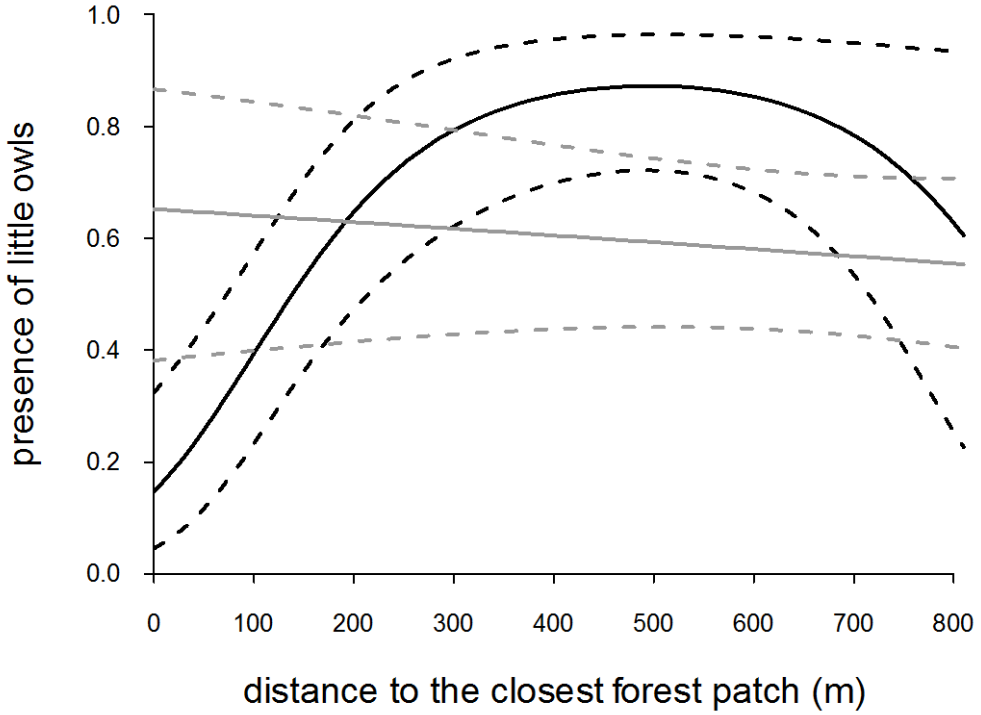

Figure 5.1. Relationship between the distance to the closest forest and the occurrence of little owls in the presence (black lines) and absence (grey lines) of tawny owls. Dashed lines represent the 95% credible interval. N = 156 playback sites

small area, the forest avoidance pattern was not as clear as at larger distances (Appendix C5, Table C5.1). The preference index revealed that beyond 50 m from the nest, areas within 150 m of the forest were avoided, while areas farther than 150 m from the forest were used according to availability or were even preferred (Fig. 5.2). The distance from the nest affected the strength of the avoidance: areas within 50 m of the forest edge were more strongly avoided when located far from (> 100 m) than close to the nest (< 100 m; Appendix C5, Table C5.1). Thus, the distance between nest and forest was an important factor modulating forest avoidance.

Direct predation

Low little owl occupancy in areas close to forests might be due to increased predation rates of little owls settling there. Out of the 167 birds observed over the course of a year, 21 birds were killed by an avian predator. Nests of the four little owls most likely killed by

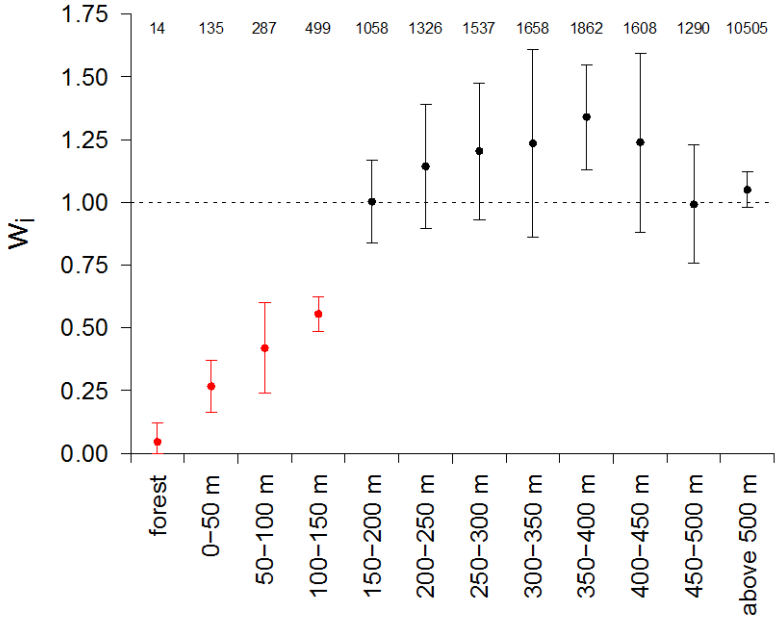

Figure 5.2. Manly's resource selection ratio W_i (use relative to availability) of distances from the forest averaged across nine distance classes from the nest (50-100 m, 100-150 m, …, 450-500 m). Points below the dashed line (W_i = 1) indicate avoidance, points above the line preference. Error bars represent the 95% confidence interval. Numbers indicate the sum of telemetry locations within each forest buffer.

tawny owls were located significantly closer to the forest than those of the other 163 little owls (mean distance ± SE: 255 ± 54 m vs. 522 ± 41 m; two-sided t-test: t = -3.944, df = 4.046, p = 0.017). When including the data of little owls killed by an unknown avian predator, the occurrence of avian predation was not significantly related to the distance of the nest to the forest (Table 5.2). Thus, little owls living close to the forest were not more

Table 5.2 Generalized linear mixed effects model (GLMM) investigating the factors affecting the occurrence of avian predation.

Predictor	Estimate	SE	CI	χ^2	P
Intercept	-4.667	2.467	-9.376 – -0.058	-	-
Sex	-0.149	0.471	-1.067 – 0.750	0.100	0.752
Distance to the forest	0.415	0.387	-0.321 – 1.167	1.191	0.275
Presence of tawny owls	0.657	0.504	-0.286 – 1.668	1.687	0.194

susceptible to avian predation than those living at larger distances. The occurrence of tawny owls did not affect the probability of little owl mortality due to avian predation, either (Table 5.2).

Vole density and habitat composition: food availability

Irrespective of the intraguild predator, differential vole abundance as well as the habitat composition near the forest might affect the range use of little owls. When controlling for habitat type, the occurrence of voles did not differ significantly between areas within 150 m of the forest and areas farther away (estimate = 0.882, CI = -1.755 – 3.485, χ^2 = 0.565, p = 0.453). However, vole abundance was shown to be higher in grassland and orchards than in arable fields (Apolloni 2013). Across our study area the relative proportion of meadows close to the forest was twice as high as the proportion at greater distances (< 150 m: 36.5%, > 150 m: 17.8%). In contrast, the relative proportion of arable fields far from the forest exceeded the proportion near the forest by half (< 150 m: 44.9%, > 150 m: 67.1%). The abundance of orchards was similar (< 150 m: 18.6%, > 150 m: 15.1%, see Appendix C5, Fig. C5.2). These results indicate an environment of higher food abundance near the forest.

Discussion

By applying different methods, we found distinct spatial patterns in a habitat-segregated intraguild predator-prey system. First, territory occupancy of the mesopredator showed a strong negative edge effect: the presence of the mesopredator rapidly decreased near forest edges in the presence but not in the absence of the top predator. Second, movement behaviour of the mesopredator showed a strong negative edge effect as well: mesopredator individuals avoided movements into areas near forest edges. Third, the availability of preferred food resources was not reduced near forest edges. In combination,

our results support the “avoidance hypothesis”: the intraguild mesopredator actively avoids the use of suitable habitats shared with a habitat segregated top predator, although these habitats would comprise preferred prey.

Edge avoidance might arise due to confounding factors such as differences in habitat composition or resource availability at habitat edges, possibly due to food depletion around habitat edges as a consequence of exploitative competition (Schoener 1983). However, there was no evidence for this “resource hypothesis”: preferred habitat types with high vole abundance (Šálek *et al.* 2010; Apolloni 2013) were more frequent within the avoided area than further from the forest, supporting the two remaining hypotheses. Since accessibility is not expected to differ between the same habitats at different distances from the forest it is unlikely that food availability is confounded by its accessibility.

The large-scale distribution of the mesopredator and its individual movement behaviour showed the same edge effect. Assuming the same underlying mechanism in range use and settlement decisions, the predator-induced edge effect likely results from predator avoidance behaviour by the mesopredator (”avoidance hypothesis”) and not from direct predation (“predation hypothesis”). The “avoidance hypothesis” is also supported by the finding that direct predation of the mesopredator was not increased at forest edges. However, we have to keep in mind that mesopredators are part of a complex multitrophic system including more than one predator. In our study system, additional intraguild top predators prey on little owls far from forest edges (e.g. common buzzard *Buteo buteo*, barn owl *Tyto alba*: Penteriani and Faivre 1997; Zuberogoitia et al. 2008), potentially blurring the effect of direct predation by the tawny owl. Mesopredators need to adapt their avoidance strategies to the type, distribution and density of different intraguild predators: habitat segregation and large scale avoidance is only possible if there are gaps in the distribution of the top predator, or if the mesopredator can resort to a habitat which is not used by the predator (Treinys *et al.* 2011; Swanson *et al.* 2014). In the absence of such

predator-free areas, the mesopredator needs to apply avoidance strategies on a small temporal or spatial scale to avoid suppression (Swanson et al. 2014). Little owls reduce their activity or move to shelter to avoid predation by barn owls co-occurring within the same habitat (Zuberogoitia et al. 2008). Here we show that little owls reduce predation risk from tawny owls through forest edge avoidance. Thus, vertebrate mesopredators not only vary in their response to the same top predator, our results suggest that a single mesopredator applies different strategies to avoid different top predators, depending on the extent of habitat segregation.

Avoidance of favored, food-rich habitats near the forest edge attests to the trade-off between costs and benefits of using edge habitat (Cresswell 2008). Our results suggest that the costs of using these areas exceed the benefits in our study area. As a result, home-ranges containing many forest edges are low in quality. The cost-benefit function of occupying habitats of different quality is expected to be density dependent (Bollinger & Switzer 2002; van Beest *et al.* 2014). As intraspecific competition increases, edge-sensitive animals are forced to use suboptimal habitats near edges (Huhta et al. 1999). Thus, whether occupancy patterns result from direct or indirect predation effects will depend on the density of both mesopredators and top predators. Within our study area, mesopredator density is low (~ 0.55 breeding pairs per km^2: H. Keil, *unpublished data*, compared to a mean density ± 1 SD of 1.84 ± 5.25 breeding pairs per km^2 across 69 western European studies: Génot and Van Nieuwenhuyse 2002) indicating that density-dependent effects are not strong enough to interfere with habitat selection. We suggest that predator-induced edge effects change from non-lethal avoidance to lethal predation with increasing mesopredator density, and that interactions and avoidance behaviour act in larger areas with increasing top predator density (St-Pierre et al. 2006).

Recent research on carnivores suggests that bottom-up effects (i.e. the density of the shared prey) determine the range use of top predators, whereas the range use of

mesopredators depends on the trade-off between predation risk and food availability (Fedriani *et al.* 2000; Heithaus 2001; Thompson & Gese 2007; Wilson *et al.* 2010; Kozlowski *et al.* 2012). Therefore, edge avoidance by habitat-segregated mesopredators likely depends on the relationship between predation risk and the distance to habitats used by top predators (Cresswell et al. 2010). The little owl, which shows a woodpecker-like flight of little maneuverability, is expected to depend on minimizing the encounter rate rather than escaping an attack. In contrast, species with more notable escape abilities are expected to use high quality habitat patches shared with the top predator despite the linked predation risk. Instead of minimizing potential encounters with a predator, they are expected to adapt their flight initiation distance to the perceived predation risk and the distance to shelter.

Habitat complexity moderates the strength of top-down effects by reducing encounter rates, by providing refuges and by improving the escape ability of prey (Janssen *et al.* 2007; Wirsing *et al.* 2010). Thus, habitat complexity promotes coexistence of intraguild predators and their prey living in the same habitat (Finke & Denno 2002; Janssen *et al.* 2007). In contrast to other studies, the top predator and mesopredator in our study system use distinct habitats and mainly interact at the edges in-between. Since landscape complexity affects the distribution and length of habitat edges, intraguild predator-prey interactions at habitat edges become a key issue at the landscape scale, particularly in the light of on-going habitat fragmentation (Haddad et al. 2015). We show that the mesopredator avoids suitable habitat along forest edges. Thus, landscape features such as size, edge-area ratio and habitat fragmentation of mesopredator habitat patches determine the impact of the intraguild predator on mesopredator populations. In contrast to the mitigating effect of habitat complexity on multitrophic interactions within habitats (Hartman et al. 2014), increasing landscape complexity is expected to reinforce

multitrophic interactions between habitats by creating edge habitat, potentially completely excluding mesopredators from suitable habitats.

Top predator induced suppression of mesopredators at habitat edges may relax the predation pressure on lower trophic levels. However, this release effect is expected to be stronger in traditional predator-prey interactions than in intraguild systems, because predation pressure by intraguild predators persists. Similar to the well-investigated "mesopredator release" (Soulé *et al.* 1988; Crooks & Soulé 1999), where the top predator is suppressed, the trophic cascades to lower trophic levels in areas of suppressed intraguild mesopredators might be complex. Further studies are necessary to elucidate whether reduced predation pressure as a result of local mesopredator suppression leads to prey release or whether the intraguild predator compensates for the reduced predation pressure.

For our study, we developed an asymmetrical, dynamic two-species occupancy model. Occupancy modeling has several advantages over analyses of home-range use based on tracking data. First, repeated assessment of occurrence at regular temporal and spatial intervals is a cost-efficient method to gather data across a large area and multiple species. The models can be extended to include additional species at different levels of food webs, integrating simultaneous information on predator and prey species. Second, it is possible to investigate change rates from one year to the next and their dependence on interspecific interactions or habitat features. Third, telemetry is often limited to individuals breeding in accessible nest boxes, whereas occupancy models based on responses to playbacks do not have this constraint. However, occupancy modeling provides no information about the mechanisms responsible for the observed patterns (Waddle et al. 2010). Therefore we suggest that future studies should combine large scale occupancy modeling with the analysis of individual behavioural data to gain deeper insights into the mechanisms shaping the spatial patterns at different trophic levels of food webs.

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References

Apolloni, N. (2013) *Landscape use, foraging habitat selection and relationships to food resources in breeding little owls: recognizing the importance of scale for species conservation management*. Thesis, Universität Bern, Bern, Switzerland.

Bates, Douglas, Maechler, Martin, Bolker, Ben, and Walker, Steven. (2014) lme4: Linear mixed-effects models using Eigen and S4. http://CRAN.R-project.org/package=lme4.

Bock, A., Naef-Daenzer, B., Keil, H., Korner-Nievergelt, F., Perrig, M. & Grüebler, M.U. (2013) Roost site selection by little owls *Athene noctua* in relation to environmental conditions and life-history stages. *Ibis*, **155,** 847-856.

Bollinger, E.K. & Switzer, P.V. (2002) Modeling the impact of edge avoidance on avian nest densities in habitat fragments. *Ecological Applications*, **12,** 1567-1575.

Brown, J.S., Laundré, J.W. & Gurung, M. (1999) The ecology of fear: Optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy*, **80,** 385-399.

Calenge, C. (2006) The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, **197,** 516-519.

Creel, S. & Christianson, D. (2008) Relationships between direct predation and risk effects. *Trends in Ecology & Evolution*, **23,** 194-201.

Cresswell, W. (2008) Non-lethal effects of predation in birds. *Ibis*, **150,** 3-17.

Cresswell, W., Lind, J. & Quinn, J.L. (2010) Predator-hunting success and prey vulnerability: Quantifying the spatial scale over which lethal and non-lethal effects of predation occur. *Journal of Animal Ecology*, **79,** 556-562.

Crooks, K.R. & Soulé, M.E. (1999) Mesopredator release and avifaunal extinctions in a fragmented system. *Nature*, **400,** 563-566.

Fedriani, J.M., Fuller, T.K., Sauvajot, R.M. & York, E.C. (2000) Competition and intraguild predation among three sympatric carnivores. *Oecologia*, **125,** 258-270.

Finke, D.L. & Denno, R.F. (2002) Intraguild predation diminished in complex-structured vegetation: Implications for prey suppression. *Ecology*, **83,** 643-652.

Fonderflick, J., Besnard, A. & Martin, J.L. (2013) Species traits and the response of open-habitat species to forest edge in landscape mosaics. *Oikos*, **122,** 42-51.

Fontaine, J.J. & Martin, T.E. (2006) Habitat selection responses of parents to offspring predation risk: An experimental test. *The American Naturalist*, **168,** 811-818.

Génot, J.-C. & Van Nieuwenhuyse, D. (2002) *Athene noctua* Little Owl. *BWP Update*, **4,** 35-63.

Giraudoux, P., Pradier, B., Delattre, P., Deblay, S., Salvi, D. & Defaut, R. (1995) Estimation of water vole abundance by using surface indices. *Acta Theriologica*, **40,** 77-96.

Gottschalk, T.K., Ekschmitt, K. & Wolters, V. (2011) Efficient placement of nest boxes for the little owl (*Athene noctua*). *Journal of Raptor Research*, **45,** 1-14.

Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers,

R.M., Foster, B.L., Jenkins, C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules, C.R., Melbourne, B.A., Nicholls, A.O., Orrock, J.L., Song, D.X. & Townshend, J.R. (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, **1,** e1500052.

Hartman, R., Pope, K. & Lawler, S. (2014) Factors mediating co-occurrence of an economically valuable introduced fish and its native frog prey. *Conservation Biology*, **28,** 763-772.

Heithaus, M.R. (2001) Habitat selection by predators and prey in communities with asymmetrical intraguild predation. *Oikos*, **92,** 542-554.

Heithaus, R. & Dill, L.M. (2006) Does tiger shark predation risk influence foraging habitat use by bottlenose dolphins at multiple spatial scales? *Oikos*, **114,** 257-264.

Huhta, E., Jokimäki, J. & Rahko, P. (1999) Breeding success of pied flycatchers in artificial forest edges: The effect of a suboptimally shaped foraging area. *The Auk*, **116,** 528-535.

Janssen, A., Sabelis, M.W., Magalhães, S., Montserrat, M. & van der Hammen, T. (2007) Habitat structure affects intraguild predation. *Ecology*, **88,** 2713-2719.

Juillard, M. (1984) *La chouette chevêche*. Nos Oiseaux, Prangins, Switzerland.

Kenward, R.E. (2001) *A manual for wildlife radio tagging*. Academic Press, London, UK.

Kéry, M. & Schaub, M. (2012) *Bayesian population analysis using WinBUGS: A hierarchical perspective*. Academic Press, Oxford, UK.

Korpimäki, E. (1987) Dietary shifts, niche relationships and reproductive output of coexisting kestrels and long-eared owls. *Oecologia*, **74,** 277-285.

Kozlowski, A.J., Gese, E.M. & Arjo, W.M. (2012) Effects of intraguild predation: Evaluating resource competition between two canid species with apparent niche separation. *Int.J.Ecol.*, **2012,** 1-12.

Lack, D. (1946) Competition for food by birds of prey. *Journal of Animal Ecology*, **15,** 123-129.

Lambin, X., Petty, S.J. & Mackinnon, J.L. (2000) Cyclic dynamics in field vole populations and generalist predation. *Journal of Animal Ecology*, **69,** 106-119.

Laundré, J.W., Hernández, L. & Altendorf, K.B. (2001) Wolves, elk, and bison: Reestablishing the "landscape of fear" in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology*, **79,** 1401-1409.

Lima, S.L. (2009) Predators and the breeding bird: Behavioural and reproductive flexibility under the risk of predation. *Biological Reviews*, **84,** 485-513.

Lima, S.L. & Dill, L.M. (1990) Behavioural decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology*, **68,** 619-640.

Lima, S.L. & Valone, T.J. (1991) Predators and avian community organization: An experiment in a semi-desert grassland. *Oecologia*, **86,** 105-112.

MacKenzie, D.I., Nichols, J.D., Hines, J.E., Knutson, M.G. & Franklin, A.B. (2003) Estimating site occupancy, colonization and local extinction when a species is detected imperfectly. *Ecology*, **84,** 2200-2207.

Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L. & Erickson, W.P. (2002) *Resource selection by animals: Statistical analysis and design for field studies*. Kluwer Academic Publishers, Nordrecht, Netherlands.

Mikkola, H. (1976) Owls killing and killed by other owls and raptors in Europe. *British Birds*, **69,** 144-154.

Morris, D.W. (2005) Paradoxical avoidance of enriched habitats: Have we failed to appreciate omnivores? *Ecology*, **86,** 2568-2577.

Naef-Daenzer, B., Früh, D., Stalder, M., Wetli, P. & Weise, E. (2005) Miniaturization (0.2 g) and evaluation of attachment techniques of telemetry transmitters. *Journal of Experimental Biology*, **208,** 4063-4068.

Navarro, J., Mínguez, E., García, D., Villacorta, C., Botella, F., Sánchez-Zapata, J.A., Carrete, M. & Giménez, A. (2005) Differential effectiveness of playbacks for little owls (*Athene noctua*) surveys before and after sunset. *Journal of Raptor Research*, **39,** 457-461.

Otsuki, H. & Yano, S. (2014) Predation risk increases dispersal distance in prey. *Naturwissenschaften*, **101,** 513-516.

Penteriani, V. & Faivre, B. (1997) Breeding density and landscape-level habitat selection of common buzzards (*Buteo buteo*) in a mountain area (Abruzzo Apennines, Italy). *Journal of Raptor Research*, **31,** 208-212.

Petty, S.J. (1999) Diet of tawny owls (*Strix aluco*) in relation to field vole (*Microtus agrestis*) abundance in a conifer forest in northern England. *Journal of Zoology*, **248,** 451-465.

Plummer, M. (2003) JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. *Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003)*, March, 20-22.

Polis, G.A. & Holt, R.D. (1992) Intraguild predation: The dynamics of complex trophic interactions. *Trends in Ecology & Evolution*, **7,** 151-154.

Polis, G.A., Myers, C.A. & Holt, R.D. (1989) The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics*, **20,** 297-330.

R Core Team. (2012) R: A language and environment for statistical computing. http://www.R-project.org.

Redpath, S.M. (1994) Censusing tawny owls *Strix aluco* by the use of imitation calls. *Bird Study*, **41,** 192-198.

Redpath, S.M. (1995) Habitat fragmentation and the individual: Tawny owls Strix aluco in woodland patches. *Journal of Animal Ecology*, **64,** 652-661.

Ries, L. & Sisk, T.D. (2004) A predictive model of edge effects. *Ecology*, **85,** 2917-2926.

Ritchie, E.G. & Johnson, C.N. (2009) Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters*, **12,** 982-998.

Šálek, M., Riegert, J. & Krivan, V. (2010) The impact of vegetation characteristics and prey availability on breeding habitat use and diet of little owls *Athene noctua* in Central European farmland. *Bird Study*, **57**.

Schoener, T.W. (1974) Resource partitioning in ecological communities. *Science*, **185,** 27-39.

Schoener, T.W. (1983) Field experiments on interspecific competition. *The American Naturalist*, **122,** 240-285.

Schönn, S., Scherzinger, W., Exo, K.-M. & Rottraut, I. (1991) *Der Steinkauz: Athene noctua*. A. Ziemsen Verlag, Wittenberg, Germany.

Soulé, M.E., Bolger, D.T., Allison, C.A., Wright, J., Sorice, M. & Hill, S. (1988) Reconstructed dynamics of rapid extinctions of Chaparral-requiring birds in urban habitat islands. *Conservation Biology*, **2,** 75-92.

St-Pierre, C., Ouellet, J.P. & Crête, M. (2006) Do competitive intraguild interactions affect space and habitat use by small carnivores in a forested landscape? *Ecography*, **29,** 487-496.

Su, Yu Sung and Yajima, Masanao. (2012) R2jags: A package for running jags from R. http://cran.r-project.org/web/packages/R2jags/index.html.

Südbeck, P., Andretzke, H., Fischer, S., Gedeon, K., Schikore, T., Schröder, K. & Sudfeldt, C. (2005) *Methodenstandards zur Erfassung der Brutvögel Deutschlands*. Vogelwarte Radolfzell, Germany.

Suhonen, J., Norrdahl, K. & Korpimäki, E. (1994) Avian predation risk modifies breeding bird community on a farmland area. *Ecology*, **75,** 1626-1634.

Sunde, P., Thorup, K., Jacobsen, L.B. & Rahbek, C. (2014) Weather conditions drive dynamic habitat selection in a generalist predator. *PLoS ONE*, **9,** e88221.

Swanson, A., Caro, T., Davies-Mostert, H., Mills, M.G.L., Macdonald, D.W., Borner, M., Masenga, E. & Packer, C. (2014) Cheetahs and wild dogs show contrasting patterns of suppression by lions. *Journal of Animal Ecology*, **83,** 1418-1427.

Thiollay, J.M. (1993) Habitat segregation and the insular syndrome in two congeneric raptors in New Caledonia, the white-bellied goshawk *Accipiter haplochrous* and the brown goshawk *A. fasciatus*. *Ibis*, **135,** 237-246.

Thompson, C.M. & Gese, E.M. (2007) Food webs and intraguild predation: Community interactions of a native mesocarnivore. *Ecology*, **88,** 334-346.

Tomé, R., Bloise, C. & Korpimäki, E. (2004) Nest-site selection and nesting success of little owls (*Athene noctua*) in Mediterranean woodland and open habitats. *Journal of Raptor Research*, **38,** 35-46.

Treinys, R., Dementavicius, D., Mozgeris, G., Skuja, S., Rumbutis, S. & Stoncius, D. (2011) Coexistence of protected avian predators: Does a recovering population of white-tailed eagle threaten to exclude other avian predators? *European Journal of Wildlife Research*, **57,** 1165-1174.

van Beest, F.M., Uzal, A., Vander Wal, E., Laforge, M.P., Contasti, A.L., Colville, D. & McLoughlin, P.D. (2014) Increasing density leads to generalization in both coarse-grained habitat selection and fine-grained resource selection in a large mammal. *Journal of Animal Ecology*, **83,** 147-156.

Van Nieuwenhuyse, D., Génot, J.-C. & Johnson, D.H. (2008) *The little owl: conservation, ecology and behaviour of Athene noctua*. Cambridge University Press, New York, USA.

Waddle, J.H., Dorazio, R.M., Walls, S.C., Rice, K.G., Beauchamp, J., Schuman, M.J. & Mazzotti, F.J. (2010) A new parameterization for estimating co-occurrence of interacting species. *Ecological Applications*, **20,** 1467-1475.

Willems, E.P. & Hill, R.A. (2009) Predator-specific landscapes of fear and resource distribution: Effects on spatial range use. *Ecology*, **90,** 546-555.

Wilson, R.R., Blankenship, T.L., Hooten, M.B. & Shivik, J.A. (2010) Prey-mediated avoidance of an intraguild predator by its intraguild prey. *Oecologia*, **164,** 921-929.

Wirsing, A.J., Cameron, K.E. & Heithaus, M.R. (2010) Spatial responses to predators vary with prey escape mode. *Animal Behaviour*, **79,** 531-537.

Zabala, J., Zuberogoitia, I., Martínez-Climent, J.A., Martínez, J.E., Azkona, A., Hidalgo, S. & Iraeta, A. (2006) Occupancy and abundance of little owl (*Athene noctua*) in an intensively managed forest area in Biscay. *Ornis Fennica*, **83,** 97-107.

Zuberogoitia, I., Martínez, J.E., Zabala, J., Martínez, J.A., Azkona, A., Castillo, I. & Hidalgo, S. (2008) Social interactions between two owl species sometimes associated with intraguild predation. *Ardea*, **96,** 109-113.

Appendix A5: Detailed methods

Playback method and procedure

Both tawny owls and little owls are highly territorial and readily respond to playbacks of conspecific territorial calls (Redpath 1994; Navarro *et al.* 2005). Suitable little owl calls were selected from the commercial CD “Eulen, Nachtschwalben & Tauben” by A. Schulze. Tawny owl calls were downloaded from the xeno-canto database (www.xeno-canto.org). Both tawny owl and little owl call bouts were composed using the program Cool Edit 2000 (Syntrillium Software Corporation, Phoenix AZ, USA) and saved as mp3 files. While the little owl playback was restricted to 20 s of calls to minimize disturbance, the tawny owl playback was composed of three call bouts of 30 second length, separated by 2 minutes of silence (according to Südbeck et al. 2005). If a little owl or a tawny owl was already calling upon arrival at the playback site, the according playback was omitted. Since calls of tawny owls might decrease the calling propensity of little owls (Zuberogoitia et al. 2008), the little owl calls were played first. Responses were recorded during 5 minutes between the little owl and the tawny owl playback and during 10 minutes after the end of the tawny owl playback. Owls generally responded in less than 5 minutes (response latency for little owls, mean ± 1 SE = 3.65 ± 0.30 min, n = 257; response latency for tawny owls = 4.96 ± 0.22 min, n = 221). For the playbacks an ION Tailgater amplifier (ION Audio LLC, Cumberland RI, USA) and an iPod touch (Apple Inc., Cupertino CA, USA) were used at a standardized volume (iPod volume at level 8, master volume at level 7).

Standardization of distance variables

The different distance variables were standardized to simplify the interpretation of the effect sizes. By subtracting half of the range and dividing by 100, variables with a mean close to 0, and an increase of 1 corresponding to 100 m distance were achieved. Following individual formulae were used: forest: x/100-4; orchard: x/100-2; village: x/100-5.

Figure A1. A 2-by-2 km grid was placed over the study area to select most of the playback sites (n = 134). 22 additional playback sites were chosen close to known little owl territories, resulting in a total of 156 playback sites. To minimize disturbance, a minimum distance of 150 m to the closest human settlement was maintained by moving twenty playback sites between 100 and 400 m from the grid points. Points located in the middle of larger cities were omitted.

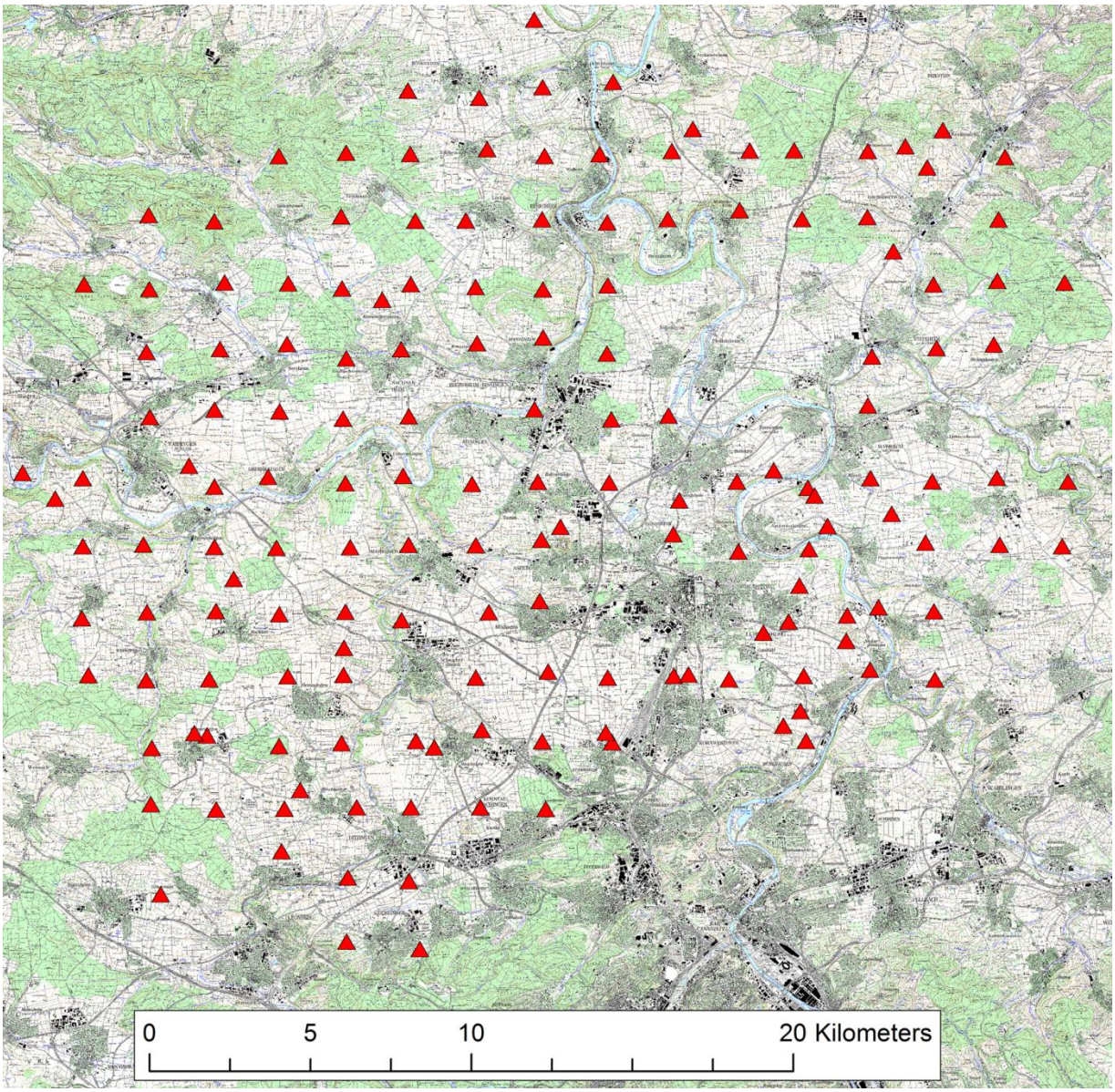

Figure A2. Procedure to calculate availability and use of areas at different forest distances. Within each distance class from the nest (0-50 m, 50-100 m, …, 450-500 m; visualized for 150-200 m from the nest boxes = pink squares), the area belonging to each forest distance buffer (dark green = inside the forest, each lighter green shading corresponding to the next 50 m buffer) was summed up. This area was divided by the amount of area at the same distance from the nest (e.g. the total area of the 150-200 m rings around all nests). Use was assessed by calculating the proportion of telemetry locations situated within each forest distance buffer. Finally, this procedure was repeated for the other nest distance classes.

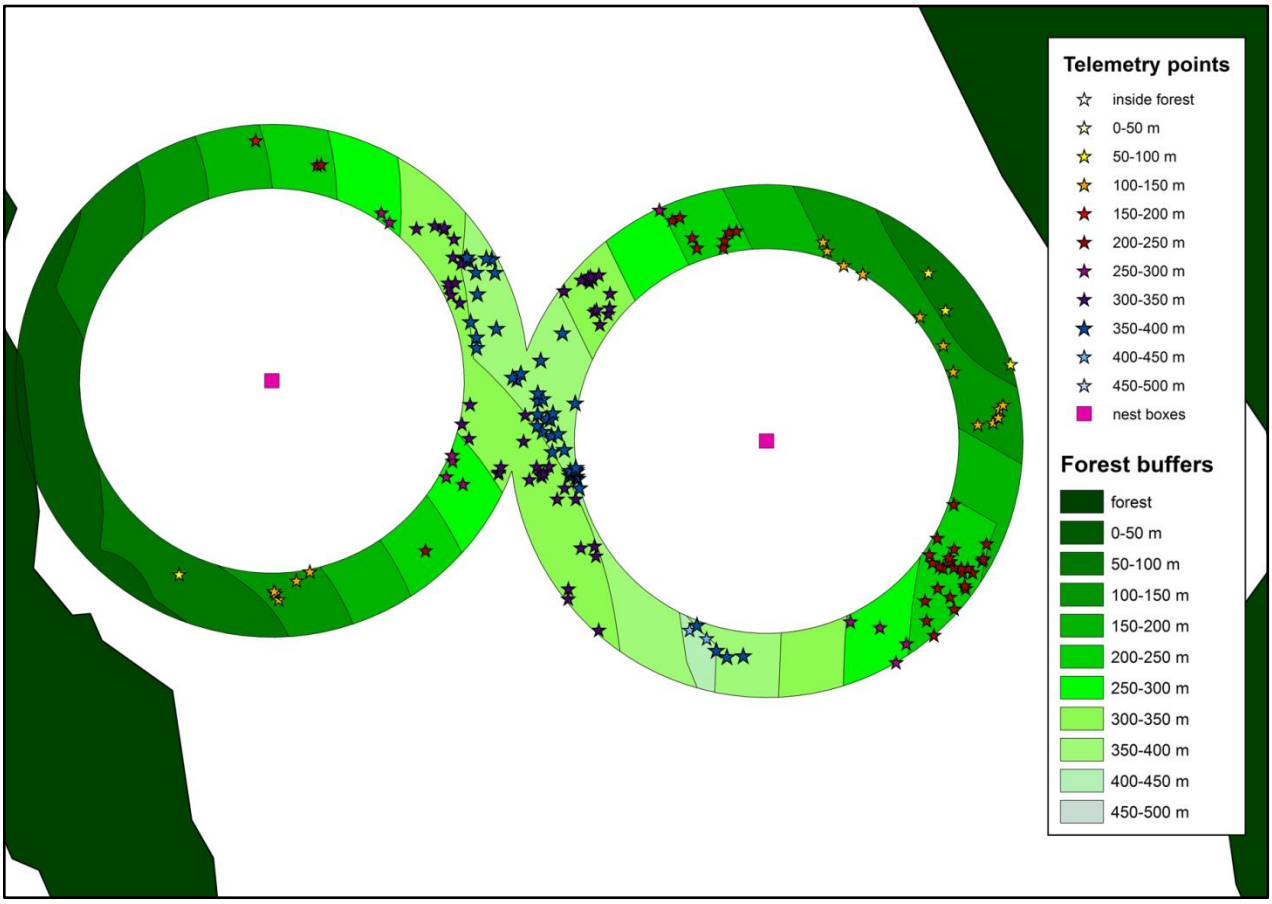

Table A5.1. Definitions of the visit-specific covariates.

Covariate	Type	Definition
Precipitation	Binary	Presence / absence of rain or snow
Wind	Binary	Presence / absence of wind
Cloudiness	Binary	More / less than 50% of the sky covered
Noise	Binary	1 = Noise levels corresponding to a heavily trafficked freeway at 150 – 300 m, or a road with intermediate traffic at 50 – 150 m

Appendix B5: Predictive model check

We performed a predictive model check to assess the prediction ability of our occupancy model. To that end, we ran the model again (100,000 iterations, 10,000 burn in, 50 thinning, and three chains) predicting a new encounter history based on the model with each simulation. Afterwards we compared the predicted with the observed data. The predicted number of sites with the different encounter histories corresponded well with the ones observed (2012: Table B5.1A, 2013: Table B5.1B). Only the number of sites with two encounters of tawny owls and no encounter of a little owl was overestimated, whereas the sites with three encounters of tawny owls and no encounter of little owls was slightly underestimated. Thus, the effective occupancy of both species was neither over- nor underestimated.

To check the prediction accuracy of the occupancy patterns, we compared occupancy dynamics determined by the predicted observation patterns with the occupancy dynamics we observed. In a mean of 76.6% of the simulations, the model predicted exactly the observed pattern for the two species within the two years. Colonization by little owls was predicted least well: in 54.2% of the simulations. Local extinction, persistence and absence were correctly predicted in 71.1%, 87.8% and 95.9% of the simulations, respectively. Only for four sites the dynamics of little owls were predicted correctly in less than 50%.

The number of sites with the different dynamics patterns of little owls was also well predicted by the model (observed data with the CrI of the simulated data in brackets: 71 (65-74) sites for absence, 20 (14-27) sites, 12 (6-17) sites, and 53 (47-62) sites.

Table B5.1. Comparison of the observed observation patterns for little owls and tawny owls with the credible interval of the simulated numbers (in brackets). The numbers indicate on how many out of three visits a species was observed. Bold print indicates over- or underestimated observation histories.

A: 2012

	Tawny owls			
Little owls	0	1	2	3
0	32 (26-37)	15 (6-21)	**13 (16-30)**	**23 (7-22)**
1	12 (4-17)	4 (0-7)	3 (1-11)	5 (0-7)
2	10 (10-22)	7 (1-9)	5 (3-13)	2 (1-9)
3	13 (4-17)	6 (0-6)	1 (1-9)	3 (0-6)

B: 2013

	Tawny owls			
Little owls	0	1	2	3
0	38 (31-45)	16 (10-27)	18 (16-32)	19 (5-19)
1	12 (4-19)	4 (0-8)	7 (1-9)	1 (0-6)
2	13 (11-23)	4 (1-8)	3 (2-10)	1 (0-7)
3	12 (4-17)	**7 (0-5)**	0 (0-6)	1 (0-4)

Appendix C5: Additional results

Figure C5.1. Posterior means of the detection probabilities of tawny owls (left panel, squares) and little owls (right panel, circles). Black symbols represent low noise levels, red symbols high noise levels. Filled squares represent detection of tawny owls in presence of wind, open squares in absence of wind. For little owls, detection probabilities in presence (filled circles) and absence (open circles) of tawny owls are illustrated. Error bars represent the 95% credible intervals.

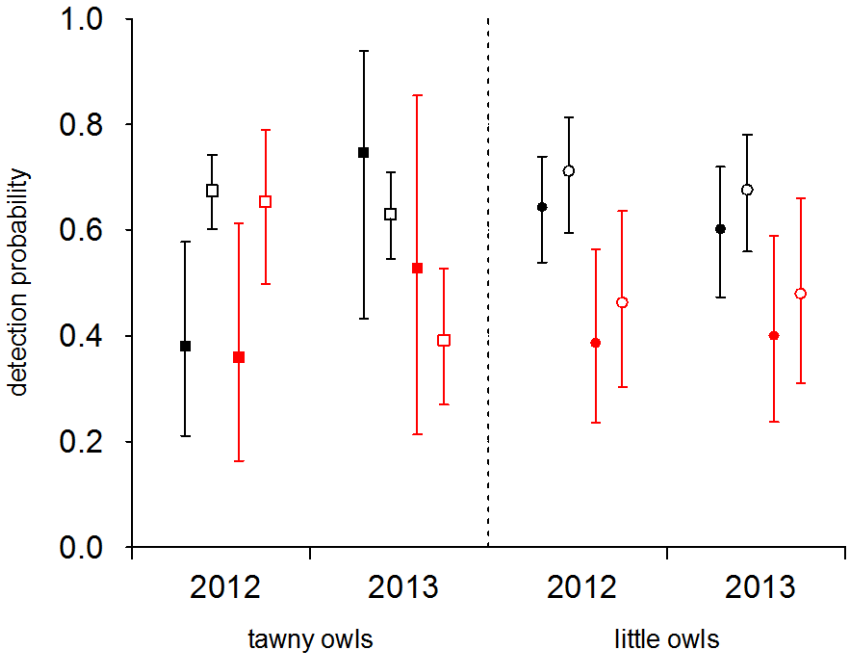

Figure C5.2. Relative proportion of arable fields (yellow), meadows (light green), and orchards (dark green) at two different distance classes from the forest.

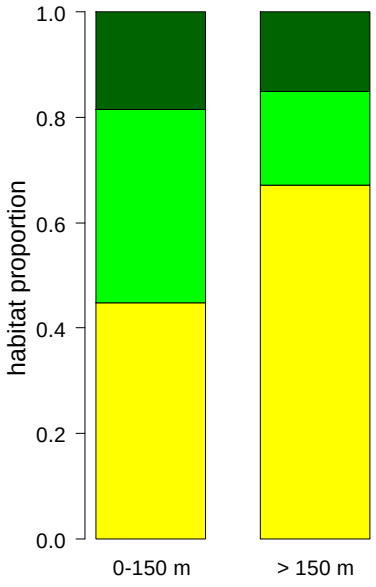

Table C5.1. Manly's resource selection ratio W_i for areas at different distances to the forest. Use and availability were compared within different distances from the nest box. Values below 1 indicate avoidance, values above 1 preference. Due to multiple comparisons, significant difference from 1 is indicated at the Bonferroni adjusted significance level of 0.00384 with light orange (avoidance) and dark green shading (selection). Numbers of locations in each distance class from the nest are indicated in the bottom line.

	Distance to the nest box (m)									
Distance to the forest (m)	0-50	50-100	100-150	150-200	200-250	250-300	300-350	350-400	400-450	450-500
0	0.00	0.23	0.37	0.00	0.00	0.00	0.00	0.14	0.02	0.00
0-50	0.67	0.51	0.22	0.22	0.25	0.18	0.26	0.27	0.32	0.17
50-100	1.43	0.59	0.28	0.17	0.55	0.48	0.55	0.26	0.47	0.49
100-150	0.63	0.54	0.58	0.66	0.41	0.48	0.63	0.56	0.53	0.58
150-200	0.73	1.07	0.95	0.99	1.16	0.84	0.81	0.59	0.78	1.78
200-250	0.74	0.93	1.10	1.44	1.17	1.20	0.99	1.46	1.60	1.05
250-300	1.20	1.00	1.04	1.36	1.43	1.26	1.40	2.02	1.16	1.30
300-350	1.09	0.97	0.94	1.28	1.19	1.48	2.12	1.31	2.20	1.92
350-400	0.96	1.20	1.31	1.17	1.26	1.70	1.34	2.47	1.93	1.32
400-450	0.70	0.87	1.47	1.36	1.27	1.03	1.11	1.25	1.81	1.80
450-500	0.88	0.76	1.03	1.11	0.85	1.15	1.10	1.13	1.64	1.24
> 500	1.09	1.10	1.01	0.94	1.02	1.11	1.12	1.10	1.02	1.16
N	12408	7124	4879	3341	2608	1999	1497	1189	1226	995

Supplement 5: Code of the dynamic two-species occupancy model

```
#############################################################################
#############################################################################
##                                                                         ##
##      R / JAGS Code of the asymmetrical dynamic two-species occupancy model      ##
##                                                                         ##
#############################################################################
#############################################################################

# load necessary package
library(R2jags)

# load data (copy the file to the current working directory)
cs <- read.table("cs.txt", header=T)
head(cs)

nsite <- 156          # number of sites
nrep <- 3             # number of repetitions
nyear <- 2            # number of years

# account for one site that was only visited twice
nrep.matrix <- matrix(nrow=nsite, ncol=nyear)
nrep.matrix[,] <- rep.int(nrep, nsite*nyear)
nrep.matrix[62,1] <- 2

# Grab and bundle data
      # Tawny owl data (Strix aluco)
sa <- array(dim = c(nsite, nrep, nyear))
sa[,1,1] <- cs[cs$species == "SA" & cs$year == 2012, "resp1"]
sa[,2,1] <- cs[cs$species == "SA" & cs$year == 2012, "resp2"]
sa[,3,1] <- cs[cs$species == "SA" & cs$year == 2012, "resp3"]
sa[,1,2] <- cs[cs$species == "SA" & cs$year == 2013, "resp1"]
sa[,2,2] <- cs[cs$species == "SA" & cs$year == 2013, "resp2"]
sa[,3,2] <- cs[cs$species == "SA" & cs$year == 2013, "resp3"]

      # Little owl data (Athene noctua)
an <- array(dim = c(nsite, nrep, nyear))
an[,1,1] <- cs[cs$species == "AN" & cs$year == 2012, "resp1"]
an[,2,1] <- cs[cs$species == "AN" & cs$year == 2012, "resp2"]
an[,3,1] <- cs[cs$species == "AN" & cs$year == 2012, "resp3"]
an[,1,2] <- cs[cs$species == "AN" & cs$year == 2013, "resp1"]
an[,2,2] <- cs[cs$species == "AN" & cs$year == 2013, "resp2"]
an[,3,2] <- cs[cs$species == "AN" & cs$year == 2013, "resp3"]
```

```
noise <- array(dim = c(nsite, nrep, nyear))
noise[,1,1] <- cs[cs$species =="SA" & cs$year == 2012, "noise1"]
noise[,2,1] <- cs[cs$species =="SA" & cs$year == 2012, "noise2"]
noise[,3,1] <- cs[cs$species =="SA" & cs$year == 2012, "noise3"]
noise[,1,2] <- cs[cs$species =="SA" & cs$year == 2013, "noise1"]
noise[,2,2] <- cs[cs$species =="SA" & cs$year == 2013, "noise2"]
noise[,3,2] <- cs[cs$species =="SA" & cs$year == 2013, "noise3"]
noise[62,3,1] <- 1

wind <- array(dim = c(nsite, nrep, nyear))
wind[,1,1] <- cs[cs$species =="SA" & cs$year == 2012, "wind1"]
wind[,2,1] <- cs[cs$species =="SA" & cs$year == 2012, "wind2"]
wind[,3,1] <- cs[cs$species =="SA" & cs$year == 2012, "wind3"]
wind[,1,2] <- cs[cs$species =="SA" & cs$year == 2013, "wind1"]
wind[,2,2] <- cs[cs$species =="SA" & cs$year == 2013, "wind2"]
wind[,3,2] <- cs[cs$species =="SA" & cs$year == 2013, "wind3"]
wind[62,3,1] <- mean(wind[,3,1], na.rm=T)

forest <- cs[cs$species =="SA" & cs$year == 2012, "forest"]
forest.sq <- forest^2

city <- cs[cs$species =="SA" & cs$year == 2012, "city"]



# Select data for model
win.data <- list(sa = sa, an = an, noise = noise, wind = wind, forest = forest,
                 forest.sq = forest.sq, city = city, nsite = nsite, nyear = nyear,
                 nrep.matrix = nrep.matrix)

# Specify model in BUGS language
modelFilename = 'model.txt'
cat("
   model {
   # ----------------- Model for tawny owls ------------------
   # Priors
   alpha.psi.sa ~ dunif(-10, 10)
   beta.forest.psi.sa ~ dunif(-10, 10)

   for (k in 1:(nyear)){
      alpha.p.sa[k] ~ dunif(-10, 10)
      beta.noise.p.sa[k] ~ dunif(-10, 10)
      beta.wind.p.sa[k] ~ dunif(-10, 10)}

   for (k in 1:(nyear-1)){
      alpha.phi.sa[k] ~ dunif(-10, 10)
```

```
    alpha.gamma.sa[k] ~ dunif(-10, 10)
    beta.forest.phi.sa[k] ~ dunif(-10, 10)
    beta.forest.gamma.sa[k] ~ dunif(-10, 10)
    beta.city.phi.sa[k] ~ dunif(-10, 10)}

# Ecological model
for (i in 1:nsite){
    z.sa[i,1] ~ dbern(psi.sa.1[i])
    logit(psi.sa.1[i]) <- alpha.psi.sa + beta.forest.psi.sa * forest[i]

for (k in 2:nyear){
    muZ.sa[i,k]<- z.sa[i,k-1] * phi.sa[i,k-1] + (1-z.sa[i,k-1]) * gamma.sa[i,k-1]
    logit(phi.sa[i,k-1]) <- alpha.phi.sa[k-1] + beta.forest.phi.sa[k-1] * forest[i] +
    beta.city.phi.sa * city[i]
    logit(gamma.sa[i,k-1]) <- alpha.gamma.sa[k-1] + beta.forest.gamma.sa[k-1] * forest[i]
    z.sa[i,k] ~ dbern(muZ.sa[i,k])
    } #k
} #i


# Observational submodel
for (i in 1:nsite){
    for (k in 1:nyear){
        for (j in 1:nrep.matrix[i,k]){
            muy.sa[i,j,k] <- z.sa[i,k] * p.sa[i,j,k]
            logit(p.sa[i,j,k]) <- alpha.p.sa[k] +
            beta.wind.p.sa[k] * wind[i,j,k] +
            beta.noise.p.sa[k] * noise[i,j,k]
            sa[i,j,k] ~ dbern(muy.sa[i,j,k])
        } #j
    } #k
} #i

# ----------------- Model for little owls ------------------
# Priors
alpha.psi.an.with ~ dunif(-10, 10)
alpha.psi.an.without ~ dunif(-10, 10)
beta.forest.psi.an.with ~ dunif(-10, 10)
beta.forest.psi.an.without ~ dunif(-10, 10)
beta.forest.sq.psi.an.with ~ dunif(-10, 10)

for (k in 1:nyear){
    alpha.p.an.with[k] ~ dunif(-10, 10)
    alpha.p.an.without[k] ~ dunif(-10, 10)
    beta.noise.p.an[k] ~ dunif(-10, 10)}
```

```
    for (k in 1:(nyear-1)){
      phi.an.with[k] ~ dunif(0,1)
      phi.an.without[k] ~ dunif(0,1)
      gamma.an.with[k] ~ dunif(0,1)
      gamma.an.without[k] ~ dunif(0,1)}

    # Ecological submodel: Initial state and observation for season k=1
    for (i in 1:nsite){
      z.an[i,1] ~ dbern(psi.an.1[i])
      logit(psi.an.1[i]) <- z.sa[i,1] * alpha.psi.an.with + (1 - z.sa[i,1]) * alpha.psi.an.without +
                            z.sa[i,1] * beta.forest.psi.an.with * forest[i] +
                            (1 - z.sa[i,1])* beta.forest.psi.an.without * forest[i] +
                            z.sa[i,1] * beta.forest.sq.psi.an.with * forest.sq[i]

      for (k in 2:nyear){
        muZ.an[i,k]<-  z.sa[i,k-1] * z.an[i,k-1] * phi.an.with[k-1] +
                       (1 - z.sa[i,k-1]) * z.an[i,k-1] * phi.an.without[k-1] +
                       z.sa[i,k-1] * (1-z.an[i,k-1])*gamma.an.with[k-1] +
                       (1 - z.sa[i,k-1]) * (1-z.an[i,k-1])*gamma.an.without[k-1]
        z.an[i,k] ~ dbern(muZ.an[i,k])
      } #k
    } #i

    # Observational submodel
    for (i in 1:nsite){
      for (k in 1:nyear){
        for (j in 1:nrep.matrix[i,k]){
          muy.an[i,j,k] <- z.an[i,k] * p.an[i,j,k]
          logit(p.an[i,j,k]) <-  z.sa[i,k] * alpha.p.an.with[k] + (1 - z.sa[i,k]) *
                                 alpha.p.an.without[k] + beta.noise.p.an[k] * noise[i,j,k]
          an[i,j,k] ~ dbern(muy.an[i,j,k])
        } #j
      } #k
    } #i

    }
    ",fill = TRUE, file=modelFilename)

# Initial values
zst.sa <- apply(sa, c(1,3), max, na.rm = TRUE)
zst.an <- apply(an, c(1,3), max, na.rm = TRUE)
zst.sa[zst.sa == -Inf] <- 0
zst.an[zst.an == -Inf] <- 0
inits <- function(){list(z.sa = zst.sa, z.an = zst.an)}
```

```
# Parameters monitored
params <-  c("alpha.psi.sa",
             "beta.forest.psi.sa",
             "alpha.p.sa",
             "beta.noise.p.sa",
             "beta.wind.p.sa",
             "alpha.phi.sa",
             "alpha.gamma.sa",
             "beta.forest.phi.sa",
             "beta.city.phi.sa",
             "beta.forest.gamma.sa",
             "alpha.psi.an.with",
             "alpha.psi.an.without",
             "beta.forest.psi.an.with",
             "beta.forest.psi.an.without",
             "beta.forest.sq.psi.an.with",
             "phi.an.with",
             "phi.an.without",
             "gamma.an.with",
             "gamma.an.without",
             "alpha.p.an.with",
             "alpha.p.an.without",
             "beta.noise.p.an",
             "z.sa",
             "z.an")

# MCMC settings
ni <- 1000000
nt <- 10
nb <- 100000
nc <- 3

# Call JAGS from R
system.time(final <- jags(win.data, inits, params, "model.txt", n.chains = nc,
                          n.thin = nt, n.iter = ni, n.burnin = nb))
```

General discussion

In this thesis I investigated the behavioural responses of adult little owls (*Athene noctua*) to environmental conditions and their fitness consequences. I focused on three important issues faced by adult animals in the course of their life: (1) the trade-off in allocating resources to reproduction and self-maintenance, (2) the decision between philopatry and breeding dispersal, and (3) the behavioural response to predation risk. Therefore, I combined observations of natural variation in habitat quality, particularly food resources**,** with experimental food supplementation to the nestlings. Following the individuals with telemetry provided home-range sizes, site fidelity, and survival rates of the adults, whereas playbacks across the whole study area provided information on predator avoidance.

The results provide insights into the fundamental determinants of spatio-temporal variation in settlement decisions and productivity of little owls, thereby contributing to the understanding of environmental effects on key demographic parameters. Among the different aspects of the environment, trophic interactions seem to play the most important role: On one hand, the availability of food affects parental foraging performance, which, in turn, determines the flow of energy to the brood as well as the reproductive output. On the other hand, predators of little owls have strong non-lethal effects, particularly on habitat selection and settlement decisions.

Energetic trade-offs

According to life-history theory, one of the most fundamental trade-offs for adult animals is the allocation of limited energy among reproduction and self-maintenance (Stearns 1989; Martin 1995). Since individuals need to acquire energy from profitable food sources within the environment, habitat quality is expected to strongly influence an individual's energy income and allocation to life-history functions (Eldegard & Sonerud 2010). Therefore, I

investigated how little owls adjust home-range size to habitat quality and how this affects their reproductive success (Chapter 1). In the same context, I analysed prey types and food provisioning rates during brood rearing (Chapter 2), and the factors affecting little owl survival (Chapter 3).

In Chapter 1, I showed that clutch size was positively correlated with the proportion of food-rich habitat close to the nest, irrespective of the home-range size of the parents. Experimental food supplementation strongly affected juvenile survival and condition. These results suggest that the distance between high quality food resources and suitable nest sites (i.e. landscape complementation: Dunning *et al.* 1992), plays an important role for the productivity of little owls.

In addition, nestling survival was positively correlated with paternal home-range size, which, in turn, was inversely linked to habitat heterogeneity. In homogenous landscapes dominated by agricultural fields, parents seem to expand their home-range to include additional food-rich habitat (resource supplementation: Dunning *et al.* 1992). The analysis of adult survival rates (Chapter 3) revealed that male survival was positively correlated with home-range size, suggesting that larger home-ranges yield a net benefit in terms of reproductive success and parental survival.

Previous studies have shown that the growth performance and survival of little owl nestlings is food-limited (Thorup *et al.* 2010; Perrig 2015). The analysis of the feeding rates in Chapter 2 showed that the total biomass brought to the nestlings depended on the quality of the habitat: nestlings in poor habitats received only two thirds of the biomass delivered to nests in high-quality habitats. In addition, the food supplementation experiment allowed me to show that little owl parents are limited by food resources, as well: Food supplementation increased the survival of both males and females, not only during the breeding season but also during the following periods of the year (Chapter 3).

As a result, food supplementation also increased individual fitness by elevating the chances for future reproduction.

A recent food-supplementation study on little owls (Jacobsen *et al.* 2016) shows that both parents reduce their foraging effort in response to additional food. Furthermore, the results from Chapter suggest that the composition of prey items brought to the nest differs between supplemented and unsupplemented broods: Parents of supplemented broods brought a larger proportion of small insects to the nest. Foraging on insects may alter the ratio between effort and benefit in favour of parents.

Thus, the first three chapters of this thesis provide insights into the multiple trade-offs between current reproduction and self-maintenance, which is also linked to future survival and reproductive prospects. In low-quality habitats, parents incur strong survival costs of reproduction. I conclude from the results that habitats of low quality have strong effects on individual life-histories and local demographic rates. In the short term, parents breeding in low-quality habitats incur high costs, whereas their reproductive output is reduced. In the long term, reduced survival prospects of adult birds living in low-quality habitats imply a marked reduction of lifetime reproductive success, and thus, fitness.

Breeding dispersal

Adult birds surviving to the next breeding season face the decision whether to stay at the same site for a subsequent reproductive attempt, or to move to a different territory. In chapter 4, I showed that the propensity of an individual to disperse was strongly affected by the achieved reproductive success. Unsuccessful individuals were more than twice as likely to disperse as successful individuals. Since habitat quality has an effect on reproductive success, it might indirectly affect the breeding dispersal rate. On the other hand, mortality of a parent drastically reduces the flow of energy to the nest, thereby affecting survival and condition of the nestlings (Chapter 1). Therefore, reproductive failure

may often be linked to mate loss. In that event, breeding dispersal may improve the chances to re-mate. In case of predation, moving away from the area might also reduce the predation risk of the surviving parent.

Predation

Within our study area, a high proportion of the mortalities are caused by predation (Naef-Daenzer *et al.* 2016). The results given in Chapter 5 suggest that little owls perceive this predation risk and adapt their spatial behaviour accordingly. Site occupancy of little owls strongly decreases within 150 m from the forest in presence, but not in the absence of tawny owls. In addition, little owls strongly avoid areas closer than 150 m to forest edges during their night-time range use. Moreover, I found some evidence for lower persistence of little owl territories in the presence of tawny owls. These results suggest that little owls actively avoid forest edges in response to predation risk.

Conclusions

I draw two main conclusions from this PhD thesis. First, it provides correlational and experimental evidence for the importance of food supply during the breeding season for both juveniles and adults. Besides the availability of food, its distribution across the landscape also plays an important role. High proportions of food-rich habitat in close vicinity to suitable nest sites strongly increase the productivity and survival. On the individual level, nest site selection determines the amount of landscape complementation and landscape supplementation, thereby also determining the access to resources. The observed variation in territory quality and its strong effect on reproductive success and parental survival suggest that settlement decisions and habitat selection represent key ecological mechanisms affecting individual fitness. As a consequence, agricultural landscapes may strongly differ in their ability to sustain viable little owl populations.

Second, results from chapters 4 and 5 suggest that habitat characteristics and the presence of predators strongly influence the spatial distribution and dynamics of little owls. Site-occupancy patterns suggest that little owls settle in areas, which minimize predation and provide them with access to optimal food resources. Breeding dispersal mainly occurred in response to reproductive failure. If specific environmental conditions are alter the risk of brood loss (e.g. presence of nest predators), these environmental aspects may further affect local population structure and dynamics. In conclusion, the results provide insights into the ecological mechanisms that shape the spatial distribution and the turn-over of individuals within a population.

References

Dunning, J.B., Danielson, B.J. & Pulliam, H.R. (1992) Ecological processes that affect populations in complex landscapes. *Oikos*, **65,** 169-175.

Eldegard, K. & Sonerud, G.A. (2010) Experimental increase in food supply influences the outcome of within-family conflicts in Tengmalm's owl. *Behavioral Ecology and Sociobiology*, **64,** 815-826.

Gottschalk, T.K., Ekschmitt, K. & Wolters, V. (2011) Efficient placement of nest boxes for the little owl (*Athene noctua*). *Journal of Raptor Research*, **45,** 1-14.

Jacobsen, L.B., Chrenková, M., Sunde, P., Šálek, M. & Thorup, K. (2016) Effects of food provisioning and habitat management on spatial behaviour of little owls during the breeding season. *Ornis Fennica*, **93,** 121-129.

Martin, T.E. (1995) Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs*, **65,** 101-127.

Naef-Daenzer, B., Korner-Nievergelt, F., Fiedler, W. & Grüebler, M.U. (2016) Bias in ring-recovery studies: causes of mortality of little owls (*Athene noctua*) and implications for population assessment. *Journal of Avian Biology*.

Perrig, M. (2015) *Juvenile survival and onset of natal dispersal in little owls (Athene noctua) in relation to nestling food supply*. PhD thesis, University of Zurich, Zurich, Switzerland.

Stearns, S.C. (1989) Trade-offs in life-history evolution. *Functional Ecology*, **3,** 259-268.

Thorup, K., Sunde, P., Jacobsen, L.B. & Rahbek, C. (2010) Breeding season food limitation drives population decline of the little owl *Athene noctua* in Denmark. *Ibis*, **152**.

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Publications, presentations and posters

Publications

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Presentations

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Posters

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